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ON FORCE-FREE MAGNETIC FIELDS

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1. *Introduction.*—Lüst and Schlüter[1] have recently pointed out that cosmic magnetic fields might often satisfy the condition

$$\text{curl } \boldsymbol{H} \times \boldsymbol{H} = 0, \tag{1}$$

where $\boldsymbol{H}$ denotes the intensity of the magnetic field. The reason for this, essentially, is that on account of the high electrical conductivity of stellar material of even low density, large currents can flow in the space surrounding the stars; the usual assumption (appropriate only for a vacuum) that the current density j should vanish outside the photospheres of stars ceases to be even an approximate description of the true state of affairs. Under the circumstances existing, it would be more accurate to say that the prevailing magnetic field is such that the Lorentz force

$$\mathfrak{L} = j \times \boldsymbol{H} = \frac{1}{4\pi} \text{curl } \boldsymbol{H} \times \boldsymbol{H} \tag{2}$$

vanishes. The presence of the magnetic field will not, then, affect the motions, and a stationary state can be envisaged.

Fields which satisfy equation (1) will be called *force-free.*

The force-free condition (1) clearly requires that

$$\text{curl } \boldsymbol{H} = \alpha \boldsymbol{H}, \tag{3}$$

where α is some function of position. The case when $\boldsymbol{H}$ has symmetry about an axis and α is a constant is of considerable practical interest. It is the case which Lüst and Schlüter have studied in some detail; but they have failed to notice that for this case the problem admits an explicit solution. It is the object of this paper to present this solution.

2. *The Basic Differential Equations.*—A magnetic field none of whose components are azimuth-dependent can always be expressed as the sum of a toroidal and a poloidal field in the form

$$\boldsymbol{H} = \mathbf{1}_z \times r\boldsymbol{T} + \text{curl } (\mathbf{1}_z \times r\boldsymbol{P}), \tag{4}$$

where $\mathbf{1}_z$ is a unit vector in the direction of the axis of symmetry (which we shall assume to be the z-axis) and P and T are any two functions which do not depend

on the azimuthal angle φ. [Note that for $\boldsymbol{H}$ defined as in equation (4) the condition div $\boldsymbol{H} = 0$ is identically satisfied.] We shall consider P and T as functions of either r and ϑ (in spherical polar co-ordinates) or ϖ and z (in cylindrical polar co-ordinates).

In cylindrical polar co-ordinates, $\boldsymbol{H}$ given by equation (4) takes the form

$$\boldsymbol{H} = -\varpi \frac{\partial P}{\partial z} \mathbf{1}_{\varpi} + \varpi T \mathbf{1}_{\varphi} + \frac{1}{\varpi} \frac{\partial}{\partial \varpi} (\varpi^2 P)\, \mathbf{1}_z, \tag{5}$$

where $\mathbf{1}_{\varpi}$ and $\mathbf{1}_{\varphi}$ are unit vectors in the radial (ϖ) and the transverse (φ) directions. For $\boldsymbol{H}$ given by equation (5) it can be readily verified that

$$\text{curl } \boldsymbol{H} = -\varpi \frac{\partial T}{\partial z} \mathbf{1}_{\varpi} - \varpi \Delta_5 P \mathbf{1}_{\varphi} + \frac{1}{\varpi} \frac{\partial}{\partial \varpi} (\varpi^2 T)\, \mathbf{1}_z, \tag{6}$$

where

$$\Delta_5 = \frac{\partial^2}{\partial \varpi^2} + \frac{3}{\varpi} \frac{\partial}{\partial \varpi} + \frac{\partial^2}{\partial z^2} \tag{7}$$

is the operator defining the axially symmetric wave equation in five dimensions. From a comparison of equations (5) and (6) it follows that condition (3) requires

$$\alpha \text{ grad } \varpi^2 P = \text{grad } \varpi^2 T \tag{8}$$

and

$$\Delta_5 P = -\alpha T. \tag{9}$$

A further condition is that grad $\varpi^2 P$ and grad α are in the same direction. This can be deduced as follows: Taking the divergence of equation (3), we obtain

$$\text{grad } \alpha \cdot \boldsymbol{H} = 0. \tag{10}$$

Substituting for $\boldsymbol{H}$ from equation (5) and remembering that grad α has components only in the ϖ- and the z-directions, we have

$$\frac{\partial \alpha}{\partial \varpi} \frac{\partial}{\partial z} (\varpi^2 P) - \frac{\partial \alpha}{\partial z} \frac{\partial}{\partial \varpi} (\varpi^2 P) = 0. \tag{11}$$

An equivalent form of this last equation is

$$\text{grad } \varpi^2 P \times \text{grad } \alpha = 0; \tag{12}$$

and this is the condition stated.

3. *The Case α = Constant.*—In this case equation (12) is clearly fulfilled, while equation (8) requires that

$$\alpha \varpi^2 P = \varpi^2 T + \text{constant}. \tag{13}$$

From equation (5) it is evident that an additive constant in $\varpi^2 P$ has no physical consequence. We may therefore assume without loss of generality that

$$\alpha P = T. \tag{14}$$

Equation (9) now becomes

$$\Delta_5 P = -\alpha^2 P. \tag{15}$$

In spherical polar co-ordinates this equation for P is

$$\left(\frac{\partial^2}{\partial r^2} + \frac{4}{r}\frac{\partial}{\partial r} + \frac{1-\mu^2}{r^2}\frac{\partial^2}{\partial \mu^2} - \frac{4\mu}{r^2}\frac{\partial}{\partial \mu} + \alpha^2\right) P = 0, \tag{16}$$

where $\mu = \cos\vartheta$.

Separable solutions of equation (16) exist, and the general solution can be expressed in terms of the fundamental solutions

$$P_n = \frac{\mathfrak{C}_{n+3/2}(\alpha r)}{r^{3/2}} C_n^{3/2}(\mu), \tag{17}$$

where $C_n^{3/2}(\mu)$ denotes the Gegenbauer polynomials[2] and $\mathfrak{C}_{n+3/2}(\alpha r)$ is a general cylinder function of order $n + 3/2$ and represents an arbitrary linear combination of the Bessel functions $J_{n+3/2}(\alpha r)$ and $J_{-(n+3/2)}(\alpha r)$.

With the solution for the poloidal function P given by equation (17), we can write the corresponding magnetic field in the form (cf. eq. [5])

$$\boldsymbol{H} = \alpha(\mathbf{1}_z \times \mathbf{r})P_n - \frac{1}{\varpi^2}(\mathbf{1}_z \times \mathbf{r}) \times \text{grad } P_n\varpi^2. \tag{18}$$

In spherical polar co-ordinates the various components of $\boldsymbol{H}$ are given by

$$\boldsymbol{H} = \left\{-\frac{1}{r^2}\frac{\partial}{\partial \mu}[P_n r^2(1-\mu^2)], \frac{-1}{r\sqrt{(1-\mu^2)}}\frac{\partial}{\partial r}[P_n r^2(1-\mu^2)], \alpha r\sqrt{(1-\mu^2)}P_n\right\}. \tag{19}$$

4. *The Boundary Conditions.*—The conditions to be satisfied at an interface where α has a jump are (1) that $\boldsymbol{H}$ should be continuous and (2) that the normal component of the current density $\boldsymbol{j}$ should also be continuous. The latter condition requires the continuity of the normal component of curl $\boldsymbol{H}$. Since curl $\boldsymbol{H} = \alpha\boldsymbol{H}$, the second condition requires the continuity of the normal component of $\alpha\boldsymbol{H}$. On the other hand, the first condition requires that the normal component of $\boldsymbol{H}$ be continuous. Since α changes discontinuously at an interface, the two conditions can be simultaneously met only if the normal component of $\boldsymbol{H}$ vanishes. The conditions at an interface are, therefore,

$$H_r = 0 \quad \text{and} \quad H_\vartheta \quad \text{and} \quad H_\varphi \quad \text{are continuous.} \tag{20}$$

From equation (19) it follows that the vanishing of H_r at $r = R$ (say) can be met only if

$$\mathfrak{C}_{n+3/2}(\alpha R) = 0, \tag{21}$$

i.e., if αR is a zero of the chosen cylinder function. If the region in question extends from $r = R_1$ to $r = R_2$, then the linear combination of $J_{n+3/2}$ and $J_{-(n+3/2)}$ should be such that it vanishes at $r = R_1$ and $r = R_2$. Such cylinder functions for various initially assigned values of R_2/R_1 have been explicitly characterized in another connection.[3]

According to equation (19), the φ-component of $\boldsymbol{H}$ vanishes, together with H_r, on an interface. Finally, the continuity of H_ϑ requires that

$$\frac{d}{dr}\left\{r^{1/2}\mathcal{C}_{n+1/2}(\alpha r)\right\} \tag{22}$$

be continuous on an interface. Since the foregoing is a linear combination of $\mathcal{C}_{n+1/2}(\alpha r)$ and $\alpha\mathcal{C}'_{n+1/2}(\alpha r)$ and the former vanishes for $r = R$ (cf. eq.[21])it is clear that the required condition is

$$\alpha\mathcal{C}'_{n+1/2}(\alpha r) \qquad \text{is continuous at an interface.} \tag{23}$$

It can be verified that the conditions found by Lüst and Schlüter in their paper refer (in our present terminology) to the special case $n = 0$.

5. *The Energy in the Magnetic Field.*—A quantity of interest is the energy in the magnetic field,

$$E = \frac{1}{8\pi}\int_{R_1}^{R_2}\int_{-1}^{+1}\int_{0}^{2\pi} |\boldsymbol{H}|^2 r^2\, dr\, d\mu\, d\varphi$$

$$= \frac{1}{4}\int_{R_1}^{R_2}\int_{-1}^{+1} |\boldsymbol{H}|^2 r^2\, dr\, d\mu. \tag{24}$$

Since the toroidal and poloidal parts of $\boldsymbol{H}$ are at right angles to each other,

$$|\boldsymbol{H}|^2 = \alpha^2 r^2 \sin^2\vartheta\, P_n^2 + |\operatorname{curl}(\mathbf{1}_z \times \boldsymbol{r}P_n)|^2. \tag{25}$$

The contribution to E from the toroidal part is readily evaluated. We have

$$E_T = \frac{1}{4}\alpha^2\int_{R_1}^{R_2} dr\, r\mathcal{C}^2_{n+1/2}(\alpha r)\int_{-1}^{+1} d\mu\,(1-\mu^2)[C_n^{3/2}(\mu)]^2. \tag{26}$$

Using the orthogonality property of the Gegenbauer polynomials[4] and of the cylinder functions, we have

$$E_T = \frac{1}{4}\alpha^2\frac{\pi(n+1)(n+2)}{2^2(n+3/2)[\Gamma(3/2)]^2}N_{j;\,n+1/2}, \tag{27}$$

where $N_{j;\,n+1/2}$ is the normalization integral for the orthogonal functions provided by the functions $\mathcal{C}_{n+1/2}(\alpha_j r)$ (cf. eq. [3] of an earlier paper[3]).

To obtain the contribution to E from the poloidal part, we proceed as follows: We have

$$E_P = \frac{1}{8\pi}\iiint \operatorname{curl}(\mathbf{1}_z \times \boldsymbol{r}P_n)\cdot\operatorname{curl}(\mathbf{1}_z \times \boldsymbol{r}P_n)\, dx_1\, dx_2\, dx_3. \tag{28}$$

By an integration by parts we get

$$E_P = \frac{1}{8\pi}\int\int_S (\mathbf{1}_z \times \boldsymbol{r}P_n) \times \operatorname{curl}(\mathbf{1}_z \times \boldsymbol{r}P_n)\cdot d\mathbf{S} +$$

$$\iiint (\mathbf{1}_z \times \boldsymbol{r})P_n \operatorname{curl}[\operatorname{curl}(\mathbf{1}_z \times \boldsymbol{r}P_n)]\, dx_1\, dx_2\, dx_3. \tag{29}$$

The surface integral vanishes on account of the boundary conditions which require P_n to be zero on the bounding surfaces (cf. eq. [21]). The remaining volume integral becomes (cf. eqs. [6] and [15])

$$E_P = -\frac{1}{8\pi}\int\int\int |\mathbf{1}_z \times \mathbf{r}|^2 P_n \Delta_5 P_n \, dx_1 \, dx_2 \, dx_3$$

$$= \frac{\alpha^2}{8\pi}\int\int\int P_n^2 r^4 (1-\mu^2)\, dr\, du\, d\varphi. \tag{30}$$

It is thus seen that *the contribution to the magnetic energy by the toroidal part and the contribution by the poloidal part are exactly equal.* Thus

$$E = 2E_P = 2E_T = \frac{1}{2}\alpha^2 \frac{\pi(n+1)(n+2)}{2^2(n+3/2)[\Gamma(3/2)]^2} N_{j;\ n+3/2}. \tag{31}$$

6. *The Equations for the Lines of Force.*—The lines of force are determined by the equations

$$\frac{dr}{H_r} = -\frac{r\, d\mu}{H_\vartheta \sqrt{(1-\mu^2)}} = \frac{r\sqrt{(1-\mu^2)}\, d\varphi}{H_\varphi}. \tag{32}$$

One integral of these equations (namely, that which follows from the first two) can be readily found. We have

$$r^{1/2}\mathfrak{C}_{n+3/2}(\alpha r)(1-\mu^2)C_n^{3/2}(\mu) = \text{constant}. \tag{33}$$

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[1] R. Lüst and A. Schlüter, "Kraftfreie Magnetfelder," *Z. Astrophys.*, **34**, 263–282, 1954.

[2] The notation is that of G. N. Watson, *A Treatise on the Theory of Bessel Functions* (Cambridge: At the University Press, 1944); see pp. 50 and 369.

[3] S. Chandrasekhar and Donna Elbert, "The Roots of $J_{-(l+1/2)}(\lambda\eta)J_{l+1/2}(\lambda) - J_{l+1/2}(\lambda\eta) \times J_{-l+1/2}(\lambda) = 0$," *Proc. Cambridge Phil. Soc.*, **49**, 446–448, 1953.

[4] Cf. A. Sommerfeld, *Partial Differential Equations of Physics* (New York: Academic Press, 1949), p. 232.

THE EQUILIBRIUM OF MAGNETIC STARS

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1. *Introduction.*—By considering a particularly simple example, Fermi and Chandrasekhar[1] showed that magnetic stars cannot, in general, be spherical. Later investigations[2] carried out with a view to establishing more concrete results have proved inconclusive. In this paper we shall prove a theorem which characterizes in a very general way the magnetic field which can prevail in an incompressible fluid in equilibrium under its own gravitation. A less complete characterization for compressible fluids is also given. The discussion is limited to configurations with an axis of symmetry.

2. *The Problem.*—The equation governing the hydrostatic equilibrium of a configuration with a prevalent magnetic field is

$$\text{grad } p = \rho \text{ grad } V + \mathfrak{L}, \tag{1}$$

where p denotes the pressure, ρ the density, V the gravitational potential, and $\mathfrak{L}$ the Lorentz force related to the current density j

$$\mathfrak{L} = j \times H. \tag{2}$$

In the usual hydromagnetic approximation,

$$j = \frac{1}{4\pi} \text{curl } H \tag{3}$$

and

$$\mathfrak{L} = \frac{1}{4\pi} \text{curl } H \times H. \tag{4}$$

Taking the curl of equation (1), we obtain

$$-\text{grad } \rho \times \text{grad } V = \text{curl } \mathfrak{L} = \frac{1}{4\pi} \text{curl } [\text{curl } H \times H]. \tag{5}$$

If we restrict ourselves to configurations with an axial symmetry (about the z-axis), so that ρ and V are azimuth-independent, the vector on the left-hand side has a nonvanishing component only in the transverse φ-direction. Consequently, curl $\mathfrak{L}$ can have no nonvanishing component in the radial (ϖ) and in the z-directions. Thus

$$(\text{curl } \mathfrak{L})_\varpi = (\text{curl } \mathfrak{L})_z = 0. \tag{6}$$

If the fluid is incompressible,

$$\text{curl } \mathfrak{L} \equiv 0, \tag{7}$$

and we must in addition require that

$$(\text{curl } \mathfrak{L})_\varphi = 0. \tag{8}$$

The problem now is: What do conditions (6) and (7) imply for the magnetic field?

3. *The Characterization of the Magnetic Field.*—We shall suppose that none of the components of the prevailing magnetic field is azimuth-dependent. We can then express the magnetic field, quite generally, as the sum of a toroidal and a poloidal field in the form (for the notation see the preceding paper[3])

$$H = (1_z \times r)T + \text{curl } (1_z \times rP), \tag{9}$$

or, in cylindrical polar co-ordinates,

$$H = -\varpi \frac{\partial P}{\partial z} 1_\varpi + \varpi T 1_\varphi + \frac{1}{\varpi} \frac{\partial}{\partial \varpi} (\varpi^2 P) 1_z. \tag{10}$$

The curl of this field is given by

$$\text{curl } \boldsymbol{H} = -\varpi \frac{\partial T}{\partial z} \mathbf{1}_{\varpi} - \varpi \Delta_5 P \mathbf{1}_{\varphi} + \frac{1}{\varpi} \frac{\partial}{\partial \varpi} (\varpi^2 T) \mathbf{1}_z, \tag{11}$$

where it may be recalled that Δ_5 is the Laplacian operator for an axially symmetric function in five-dimensional Euclidean space. The corresponding Lorentz force is given by

$$4\pi \mathfrak{L} = \left\{ -\Delta_5 P \frac{\partial}{\partial \varpi} (\varpi^2 P) - T \frac{\partial}{\partial \varpi} (\varpi^2 T) \right\} \mathbf{1}_{\varpi} + \left\{ -\frac{\partial P}{\partial z} \frac{\partial}{\partial \varpi} (\varpi^2 T) + \frac{\partial T}{\partial z} \frac{\partial}{\partial \varpi} (\varpi^2 P) \right\} \mathbf{1}_{\varphi} + \left\{ -\varpi^2 T \frac{\partial T}{\partial z} - \varpi^2 \frac{\partial P}{\partial z} \Delta_5 P \right\} \mathbf{1}_z, \tag{12}$$

and the curl of $\mathfrak{L}$ is given by

$$\text{curl } \mathfrak{L} = -\frac{\partial \mathfrak{L}_{\varphi}}{\partial z} \mathbf{1}_{\varpi} + \left(\frac{\partial \mathfrak{L} \varpi}{\partial z} - \frac{\partial \mathfrak{L}_z}{\partial \varpi} \right) \mathbf{1}_{\varphi} + \frac{1}{\varpi} \frac{\partial}{\partial \varpi} (\varpi \mathfrak{L}_{\varphi}) \mathbf{1}_z. \tag{13}$$

The vanishing of the ϖ and the z-components of curl $\mathfrak{L}$, therefore, requires that

$$\frac{\partial \mathfrak{L}_{\varphi}}{\partial z} = 0 \quad \text{and} \quad \frac{\partial}{\partial \varpi} (\varpi \mathfrak{L}_{\varphi}) = 0. \tag{14}$$

These conditions can be met by a nonsingular $\mathfrak{L}_{\varphi}$ only when

$$\mathfrak{L}_{\varphi} \equiv 0. \tag{15}$$

According to equation (12), this implies

$$\frac{\partial}{\partial \varpi} (\varpi^2 T) \frac{\partial}{\partial z} (\varpi^2 P) - \frac{\partial}{\partial z} (\varpi^2 T) \frac{\partial}{\partial \varpi} (\varpi^2 P) = 0, \tag{16}$$

or

$$\frac{\partial (\varpi^2 T, \varpi^2 P)}{\partial (\varpi, z)} = 0. \tag{17}$$

We have thus proved that *in an axially symmetric configuration in gravitational equilibrium the prevalent magnetic field should be such that*

$$\varpi^2 T = F(\varpi^2 P), \tag{18}$$

where F is a function of the specified argument.

If we suppose that the configuration is in addition incompressible, then the ϖ-component of curl $\mathfrak{L}$ should also vanish; this further condition gives (cf. eqs. [12] and [13])

$$\frac{\partial}{\partial z} \left\{ -\Delta_5 P \frac{\partial}{\partial \varpi} (\varpi^2 P) - T \frac{\partial}{\partial \varpi} (\varpi^2 T) \right\} - \frac{\partial}{\partial \varpi} \left\{ -\varpi^2 T \frac{\partial T}{\partial z} - \varpi^2 \frac{\partial P}{\partial z} \Delta_5 P \right\} = 0. \tag{19}$$

On simplifying this equation, we find that we are left with

$$\frac{\partial (\Delta_5 P, \varpi^2 P)}{\partial (\varpi, z)} = \varpi \frac{\partial T^2}{\partial z}. \tag{20}$$

The general solution of this equation can be found as follows:

First, we observe that we can define a function $G(\varpi^2 P)$ such that

$$\frac{\partial(\varpi^2 P,\ G(\varpi^2 P)/\varpi^2)}{\partial(\varpi,\ z)} = \varpi \frac{\partial T^2}{\partial z}. \tag{21}$$

For, on expanding the Jacobian on the left-hand side, we find that the equation reduces to

$$2G \frac{\partial}{\partial z}(\varpi^2 P) = \frac{\partial}{\partial z} \varpi^4 T^2. \tag{22}$$

Since $\varpi^2 T$ is a function of $\varpi^2 P$ only, the foregoing equation is equivalent to

$$2G(\varpi^2 P) = \frac{d}{d(\varpi^2 P)}(\varpi^4 T^2); \tag{23}$$

this defines the function G which will satisfy equation (21).

Returning to equation (20), we can combine it with equation (21) in the following manner:

$$\frac{\partial(\Delta_5 P + G/\varpi^2,\ \varpi^2 P)}{\partial(\varpi,\ z)} = 0. \tag{24}$$

In other words,

$$\Delta_5 P + \frac{1}{\varpi^2} G(\varpi^2 P) = \Phi(\varpi^2 P), \tag{25}$$

where Φ is an arbitrary function of the argument. Using equation (23), we can rewrite equation (25) in the form

$$\Delta_5 P = -T \frac{d}{d(\varpi^2 P)}(\varpi^2 T) + \Phi(\varpi^2 P), \tag{26}$$

which makes the relation between P and T explicit.

Equation (26) *characterizes the most general magnetic field which can prevail in an axially symmetric configuration of an incompressible fluid in gravitational equilibrium.*

If $T = 0$, equation (26) reduces to

$$\Delta_5 P = \Phi(\varpi^2 P); \tag{27}$$

this is equivalent to a condition first obtained by Ferraro,[4] who restricted himself to poloidal fields. On the other hand, if we let

$$T = \alpha P \quad \text{and} \quad \Phi = 0, \tag{28}$$

the equation reduces to

$$\Delta_5 P = -\alpha^2 P; \tag{29}$$

this is the equation characterizing force-free fields discussed in the preceding paper.

The simplest generalization of force-free fields applicable to the problem on hand is obtained by setting

$$T = \alpha P \quad \text{and} \quad \Phi = \text{constant}, \tag{30}$$

in which case

$$\Delta_5 P = -\alpha^2 P + \text{constant}. \tag{31}$$

The properties of the resulting equilibrium configurations will be investigated separately.

4. *An Application to Hydrodynamics.*—It is well known that the equations of motion of an incompressible inviscid fluid can be written in the form

$$\frac{\partial \boldsymbol{u}}{\partial t} - \boldsymbol{u} \times \operatorname{curl} \boldsymbol{u} = -\operatorname{grad}\left(\frac{p}{\rho} + \frac{1}{2}|\boldsymbol{u}|^2\right). \tag{32}$$

Accordingly, for stationary flows, the velocity field must satisfy the condition

$$\operatorname{curl}(\boldsymbol{u} \times \operatorname{curl} \boldsymbol{u}) = 0. \tag{33}$$

This is formally the same as the equation for $\boldsymbol{H}$ (cf. eqs. [5] and [7]) considered in this paper. Consequently, if we restrict ourselves to axially symmetric stationary flows and represent the velocity field as the sum of a toroidal and a poloidal field in the manner of equation (9), then the theorem included in equation (26) is applicable to the hydrodynamical problem. These remarks solve generally a problem recently considered by Lüst and Schlüter.[5]

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CHANGES IN THE COMPOSITION OF AN ACTINOMYCIN COMPLEX DURING GROWTH OF A STREPTOMYCES CULTURE

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The actinomycins thus far isolated from the culture media of certain species of *Streptomyces* have been shown to consist of a group of closely related chemical compounds composed of a quinonoid chromophore linked to a peptide.[1, 2] Physical and chemical differences observed among the various actinomycins so far described are considered to be due to variations in the number, arrangement, and kinds of amino acids present in the peptide;[2] the chromophoric moiety is believed to be identical in each of these substances.[3] The actinomycins reported in the literature have been designated as A, B, C, D, I, J, and X.[4] Paper chromatography and countercurrent distribution of these actinomycins have revealed that they are generally composed of a mixture of several components present in different proportions.[2, 4]

Whereas a number of investigations have been carried out on the isolation and characterization of the actinomycin complexes and on the classification and identification of the microörganisms producing these substances, insufficient attention has been given to the influence of nutrition and conditions of cultivation on the nature of the complex formed by a given organism. Brockmann observed[5] that the proportion of various components of an actinomycin complex was modified to some extent by changes in the nitrogen source of the organism. For example, when KNO_3 was supplied to actinomycin X–producing strains, production of actinomycin X_1 was slight, whereas with glycine the level of actinomycin X_1 in the complex increased considerably. However, in none of Brockmann's studies did a variation of cultural conditions cause a minor component to become a major one. Such a reversal in the ratio of the components of an actinomycin complex has been found during growth of a *Streptomyces* culture and is the subject of the present communication.

Streptomyces 3720, isolated from garden soil, initially was found to produce an actinomycin complex of the B type during growth on a soya peptone–glucose medium. In a subsequent experiment conducted under comparable environmental conditions, the actinomycin complex formed was identified as the I type. The sole difference between the two experiments was the length of incubation of the culture. In the first case the material was extracted from 5-day-old cultures and in the second from 7-day-old cultures. To resolve this discrepancy, a more comprehensive investigation was carried out.

Experimental.—Five milliliters of a 48-hour-old shake culture of *Streptomyces* 3720 was inoculated into 2-liter Erlenmeyer flasks each containing 500 ml. of soya peptone medium.[6] The flasks were then incubated at 28° C. on a rotary shaker. At 12-hour intervals aliquots of the broth were taken for the extraction of actinomycin. Using circular paper chromatography (solvent system: 5 per cent sodium orthocresotinate and ethyl acetate–*n*-butyl ether [2:1]), a qualitative determination of the complex was achieved. The individual zones on a paper chromatogram

were then cut out, the actinomycin eluted with acetone-water (9:1), and the relative percentage of each component in a complex calculated after photometric determination of the eluate with a Beckman DU spectrophotometer.

It can be seen (Fig. 1) that with an increase in time of incubation there is a considerable change in the relative percentage of the components found in the actinomycin complex. After 2 days' incubation the complex was of the B type; thereafter, a gradual transition took place, and by 5 days the complex was definitely of the I type.

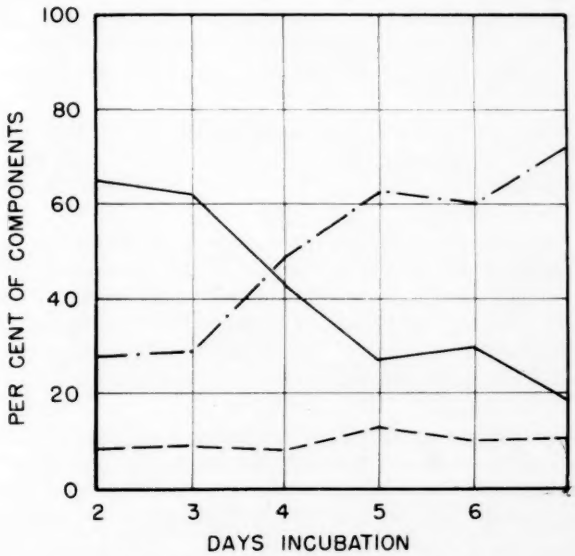

FIG. 1.—Relative per cent of the components in the actinomycin complex produced by *Streptomyces* 3720. The dashed line represents the slow-moving component, the dot-dashed line represents the intermediate component, and the solid line represents the fast-moving component on a circular paper chromatogram using a 5 per cent sodium orthocresotinate and ethyl acetate/*n*-butyl ether system.

Similar studies were performed with *Streptomyces* 3720, employing a chemically defined medium consisting of 1 per cent galactose, 0.2 per cent glutamic acid, 0.1 per cent K_2HPO_4, 0.0025 per cent $MgSO_4 \cdot 7H_2O$, 0.0025 per cent $FeSO_4 \cdot 7H_2O$, 0.0025 per cent $ZnSO_4 \cdot 7H_2O$, and 0.0025 per cent $CaCl_2 \cdot 2H_2O$ in distilled water. Once again the transition from the B- to the I-type complex occurred.

To determine whether different strains within the parent culture were responsible for the formation of the B- and I-type complexes, several colonial types found in the parental culture were isolated and grown separately in soya peptone–glucose medium. Analysis of the actinomycin produced during growth of these isolates revealed that all initially formed the B-type, and subsequently the I-type, complex. Additional studies of the parent culture as well as of the variant types derived from it are in progress. On the other hand, a preliminary investigation of *Streptomyces*

3686, an actinomycin I producer, revealed the fact that only the I-type complex was formed throughout the entire incubation period.

Unpublished data[7] on the physical and chemical properties of pure components of certain actinomycin complexes (B, D, I) have revealed that some of these are identical. Therefore, differences among certain actinomycin complexes may depend solely on the relative proportions of comparable components. As demonstrated in this preliminary report, such proportions can be modified to a considerable extent during prolonged cultivation of an organism. What factors may be operating to bring about this change are unknown at the present time. It remains to be determined whether this modification might involve an effect of the gradually changing cultural environment upon the physiological activities of the organism or whether such changes may influence the selection of specific types with different synthetic abilities.[8]

A detailed study of the culture *Streptomyces* 3720 revealed it to be a typical representative of the *S. antibioticus* group. It is to be recalled that it was a member of this group of actinomycetes that was first found[9] to produce actinomycin, later designated as "actinomycin A."

Summary.—*Streptomyces* 3720, a member of the *S. antibioticus* group, produces a significant change in the relative percentage of the components present in the actinomycin complex during growth on either a complex organic or chemically defined medium. This organism produces in the medium during the early stage of growth the actinomycin B complex. On continued incubation of the culture, the actinomycin B is changed to the actinomycin I-type complex.

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ON THE MECHANISM OF HYDROGENASE ACTION

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The biological activation of molecular hydrogen to serve as an electron or hydrogen donor is catalyzed by the enzyme hydrogenase. This enzyme, which occurs in a large variety of microörganisms, also appears to be the terminal component of the multienzyme systems responsible for photochemical formation of H_2 and for evolution of this gas in fermentations of carbohydrates, amino acids, purines, and related substances.[1] Both types of activity, i.e., oxidation and formation of hydrogen, have commonly been considered to be due to the same enzyme, particularly because certain organisms which contain hydrogenase behave as a reversible hydrogen electrode according to the following equation:[2]

$$H_2 \rightleftharpoons 2H^+ + 2e. \tag{1}$$

Recent investigations have demonstrated that electrons or hydrogen derived from activation of H_2 can readily be funneled into the well-known systems of electron transfer in which pyridine nucleotides, flavin, and cytochrome enzymes are prominent.[3, 4] For purposes of purification and for study of the properties of hydrogenase itself, however, a dye such as methylene blue is ordinarily employed as the electron acceptor in the enzyme assay. The over-all reaction in this case is

$$H_2 + \text{methylene blue} \rightarrow \text{methylene blue}\cdot 2H. \tag{2}$$

An alternative assay system developed recently[5] is based on formation of molecular hydrogen from the reduced form of the "one-electron" dye methyl viologen ($E_0' = -0.446$ volts), i.e.,

$$2 \text{ viologen}\cdot e + 2H^+ \longrightarrow H_2 + 2 \text{ viologen}. \tag{3}$$

A survey of hydrogenase preparations from a variety of organisms using the foregoing assays (reactions [2] and [3]) disclosed that both activities were usually present. Of particular significance, however, was the observation that certain hydrogenases appeared to catalyze only reaction (2).[5] These results suggested that hydrogenase may be a "double-headed" enzyme with two prosthetic groups. According to this interpretation, one prosthetic group might be considered to mediate electron transport to dyes or physiological acceptors of relatively high redox potential, while the other might be concerned with reduction of "one-electron" acceptors of low potential and also with formation of molecular hydrogen.

In addition to the reactions already noted, certain hydrogenase preparations catalyze an isotope exchange reaction between water and molecular hydrogen as in equation (4):[6]

$$HDO + H_2 \rightleftharpoons H_2O + HD. \tag{4}$$

Closely related to this activity is the ability of such preparations to catalyze the ortho-para hydrogen conversion reaction.[7]

Reaction (4) has frequently been assumed to represent a "primary" activity of hydrogenase (i.e., the immediate and direct reaction catalyzed by the enzyme itself). The data available from several recent reports, however, suggest that the velocity of the exchange reaction in certain instances (in *Azotobacter vinelandii*[8] and *Rhodospirillum rubrum*[9]) is very slow as compared with "hydrogenation" activity (i.e., reaction [2]). This apparent discrepancy indicated the desirability of a quantitative comparison of hydrogenase activities in various preparations as measured by reactions (2), (3), and (4). Recent developments in the elucidation of metallo-flavoprotein oxidation-reduction enzymes[10] also suggested the need for further study of the metal components of hydrogenase. The results of such experiments and their implications for the mechanism of hydrogenase action are reported in this communication.

EXPERIMENTAL

The crude cell-free extracts were made as described by Peck and Gest,[5] except that the *Escherichia coli* extract was prepared by disruption of the cells in a Hughes press.[11] Fraction 1 of *Micrococcus lactilyticus* was obtained by precipitation with ammonium sulfate (for details see Peck and Gest[5]); fraction 2 was derived from the same extract by further addition of ammonium sulfate to a saturation of approximately 40 per cent.

Evolution of hydrogen from reduced methyl viologen (reaction [3]) and reduction of methylene blue (reaction [2]) were measured essentially as described previously;[5] in the methylene blue assay, the center well of the Warburg vessel contained alkaline pyrogallol to remove residual traces of oxygen, and the enzyme-plus-buffer solution was supplemented with 10 mg. of crystalline albumin (Armour) per 1.2 ml.

Exchange-activity assays (reaction [4]) were conducted in vessels of the design described by Hoberman and Rittenberg.[12] The flasks were shaken at 25° C. at a rate of 130–140 strokes per minute on a reciprocal shaker with a 0.75-inch excursion. The liquid phase consisted of 10 per cent D_2O; 0.05 *M* phosphate buffer, pH 6.5; enzyme preparation; and distilled water (final volume, 5 ml.). Except for control experiments, the actual quantity of each extract tested was that showing an activity of approximately 2,500–3,000 μl. H_2 utilized per hour with methylene blue as the electron acceptor. Just before each assay, 1.3 mg. of solid sodium hydrosulfite was added (in order to deoxygenate hydrogenase[13]) to each flask; the latter was immediately evacuated and flushed twice with tank hydrogen and then filled with hydrogen to a pressure of 0.5 atmosphere. The change in deuterium content of the gas phase was measured at various intervals, using a mass spectrometer.

RESULTS AND DISCUSSION

All the preparations tested (with hydrosulfite present) showed linear exchange rates over a period of approximately 90 minutes. In the case of *Clostridium butylicum* the linear per cent D versus time curve did not pass through the origin, apparently because a small quantity of isotopic gas was released initially upon addition of hydrosulfite to the reaction mixture. In control experiments using the *E. coli* extract, it was established that the rate of exchange was proportional to

enyzme concentration under the conditions employed and therefore was not limited by the rate of hydrogen diffusion into the liquid phase.

a) Relationship of Exchange to Other Hydrogenase Activities.—The exchange activities observed in the different microbial preparations and the corresponding activities determined with the other two methods of assay (reactions [2] and [3]) are listed in Table 1.

TABLE 1

ISOTOPE EXCHANGE, HYDROGEN EVOLUTION, AND METHYLENE BLUE REDUCTION ACTIVITIES IN DIFFERENT MICROBIAL PREPARATIONS

Preparation	Isotope Exchange Assay: Increase in Atoms Per Cent Excess D/Hr/Ml	Methylene Blue Reduction Assay (μl H_2 Utilized/Hr/Ml)	Evolution Assay (μl H_2 Evolved/Hr/Ml)
M. lactilyticus:			
Crude	9.30	63,000	231,000
Fraction 1	0.18	5,520	240
Fraction 2	0.93	6,480	11,280
C. pasteurianum	10.60	70,500	147,000
C. butylicum	1.00	3,900	420,000
E. coli	1.80	16,200	22,500
A. vinelandii	0	3,720	0
R. rubrum	0	6,060	0

Thus methylene blue is readily reduced by certain preparations which do not show appreciable exchange activity, i.e., by *M. lactilyticus* (fraction 1), *A. vinelandii*, and *R. rubrum*.[14] It is significant that these particular hydrogenases also show essentially no activity by the evolution assay (reaction [3]). Rapid exchange was observed only in preparations which showed activities in both the methylene blue reduction and the evolution assays.

It may be noted that, in systems showing exchange, the ratio of evolution to reduction activity varies from approximately 2 to 4, except in the case of *C. butylicum*. The very large ratio observed with the latter preparation is due to the extreme sensitivity of this particular hydrogenase to inactivation by molecular oxygen (largely reversible) and other oxidizing agents. Thus, in contrast to other hydrogenases, reduction of methylene blue by *C. butylicum* extract can be successfully demonstrated only if very special precautions are taken to insure completely oxygen-free conditions. Molecular hydrogen is rapidly oxidized by this preparation with the one-electron dye benzyl viologen ($E_0' = -0.359$) acting as the acceptor, but again only if a low redox potential is established.[5] In the evolution assay, the powerful reducing mixture of hydrosulfite plus methyl viologen apparently reverses inactivation, due to traces of oxygen, which may occur during experimental manipulations. From this standpoint, the evolution-assay procedure offers a distinct experimental advantage, particularly since the sensitivity of most hydrogenases to inactivation by oxygen increases markedly with purification (see, e.g., Sadana and Jagannathan[15]). The conditions used in measuring the exchange reaction are not so strongly reducing as in the evolution assay, and this may account for the relatively low exchange activity shown by *C. butylicum* hydrogenase (i.e., the value listed is a minimum).

The virtual absence of exchange activity in certain preparations capable of activating H_2 for reduction of dyes suggests modification of current views on the nature of bacterial hydrogenase and on the significance of the isotope exchange reaction as a primary assay for the enzyme (see below).

b) Metal Components of Hydrogenase.—Recent experiments of Shug, Wilson, Green, and Mahler[4] have shown that MoO_3 and flavin adenine dinucleotide are required for reduction of cytochrome c by a purified hydrogenase from *C. pasteurianum*. Similar results with *M. lactilyticus* hydrogenase have been obtained by Whiteley and Ordal,[16] who studied H_2 oxidation with benzyl viologen acting as acceptor.

There is compelling evidence indicating the presence of a second metal, viz., iron, as a functional component of hydrogenase. Of particular significance in this connection is the fact that hydrogenase action is markedly inhibited by CO. This is illustrated in Table 2, which represents a compilation of data obtained by a number of investigators in studies with a variety of hydrogenase preparations.

TABLE 2

CARBON MONOXIDE INHIBITION OF HYDROGENASE ACTIVITIES

Organism	Type of Preparation	Activity Measured	Volume Per Cent CO	Per Cent Inhibition	Light Reversal	Reference
C. pasteurianum	Purified enzyme	Methylene blue reduction	20	75	None	Shug and Wilson*
C. butylicum	Purified enzyme†	H_2 evolution from methyl viologen	100	100	...	Peck and Gest†
C. butyricum	Intact cells	H_2 evolution from pyruvate	5	55	Observed	Kempner and Kubowitz;‡ Kubowitz§
			25	82		
			100	92		
E. coli	Cell-free extract	Methylene blue reduction	25	56	None	Joklik‖
			75	75		
	Intact cells	H_2 evolution from formate	100	100	...	Stephenson and Stickland#
P. vulgaris	Intact cells	Exchange reaction	50	80	Observed	Hoberman and Rittenberg**
			71.5	100		
A. vinelandii	Cell-free extract	Ferricyanide reduction	20	45	None	Hyndman, Burris and Wilson††
			25	65		

* In *Symposium on Inorganic Nitrogen Metabolism* (Baltimore: Johns Hopkins University Press) (in press).
† The specific activity of the purified enzyme was 2.5×10^6 µl H_2 evolved/hr/mg protein nitrogen at 30° C. The purification procedure and properties of the enzyme will be described in detail elsewhere.
‡ *Biochem. Z.*, **265**, 245, 1933.
§ *Biochem. Z.*, **274**, 285, 1934.
‖ *Australian J. Exptl. Biol. Med. Sci.*, **28**, 331, 1950.
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** *J. Biol. Chem.*, **147**, 211, 1943.
†† *J. Bacteriol.*, **65**, 522, 1953.

Light-reversibility of the CO inhibition, a characteristic of iron enzymes, has been reported in two instances, viz., for the production of H_2 by intact cells of *C. butyricum*[17] and for the exchange reaction in intact *Proteus vulgaris*.[12] Failure to detect light-reversibility in a number of other cases does not appear to represent a critical argument against implication of iron, since in these instances dyes and other light-absorbing substances were generally present in high concentration and could well have interfered by absorption of effective wave lengths.

Kempner and Kubowitz[17] obtained an action spectrum of the "hydrogen-evolving enzyme" in intact cells of *C. butyricum* by determining the efficiencies of CO inhibition reversal with light of different wave lengths. This spectrum has been interpreted by Warburg[18] to indicate an iron enzyme, but not one of the porphyrin type. Since the activity of purified hydrogenase from *C. butylicum* (believed to be the same organism as *C. butyricum*) is completely suppressed by CO, it appears that the inhibition studied by Kempner and Kubowitz was undoubtedly due to combination of CO with the hydrogenase enzyme rather than

to inhibition of other enzymes concerned with the fermentation of pyruvate. Similarly, the sensitivity of *E. coli* hydrogenase to CO probably also accounts for the CO inhibition of H_2 production from formate by the hydrogenlyase enzyme complex.

Stimulatory effects of Fe^{++} on hydrogenase activity in partially resolved preparations from *M. lactilyticus*[16] and *C. butylicum* (Peck and Gest, unpublished) have been noted. On the basis of all of these findings, together with those of early nutrition experiments[19] which indicated an iron requirement for the formation of the enzyme, it is concluded that iron is a functional component of hydrogenase.

c) A Suggested Formulation of Hydrogenase Action.—On the basis of experiments with *P. vulgaris*, Krasna and Rittenberg[7] have suggested that both the exchange reaction and the ortho-para interconversion are catalyzed by hydrogenase according to the following "primary" reaction:

$$H_2 + E \rightleftharpoons E{:}H^- + H^+, \tag{5}$$

where E represents the hydrogenase enzyme. In the presence of D_2O (i.e., D^+), HD would be produced by reversal of reaction (5). It may be noted that the hydrogen metabolism of *P. vulgaris* closely resembles that of *E. coli*, and, in conformity with the results already described, extracts of the former organism also show both methylene blue reduction and evolution activities.[5]

According to Krasna and Rittenberg,[7] "any organism which possesses hydrogenase activity should be capable of carrying out both the conversion of para hydrogen and the exchange reaction." The present results observed with the preparations from *M. lactilyticus* (fraction 1), *A. vinelandii*, and *R. rubrum*[14] are not consistent with their postulated mechanism.

A consideration of the available data suggests the following formulation for the mechanism of action of hydrogenase:

$$\begin{array}{ccccc} H_2 + E(Fe^{++}) \rightleftharpoons E(Fe^{++}){:}2H & \rightleftharpoons & E(Fe^{++})\text{-flavin}{:}2H \\ \downarrow \text{ flavin} & & \updownarrow \text{ Mo} \\ \text{methylene blue} & & 2 \text{ viologen}\cdot e + 2H^+ \end{array}$$

According to this scheme,[20] molecular hydrogen is activated by a ferrous enzyme to form a reduced enzyme complex. The latter can be oxidized through the agency of a flavin component by methylene blue and similar acceptors. Alternatively, if molybdenum is properly combined with the enzyme, flavin:2H can be reoxidized by one-electron acceptors such as viologen dyes.

The reduction of viologens by H_2 and formation of hydrogen from the reduced methyl dye would require the complete system, i.e., flavin and the two metals. Similarly, isotope exchange activity (i.e., conversion of D^+ to HD) would be catalyzed only by the complete system. This formulation accounts for the correlation reported here between exchange and evolution activities.

If the specific molybdenum component were absent, the hydrogenase would be capable of reacting only with methylene blue, i.e., exchange and evolution activities would not be manifested. Preparations in this category would be those from *R. rubrum*, *A. vinelandii*, and *M. lactilyticus* (fraction 1). Further support for this view is found in the fact that molybdenum is required for reduction of cytochrome c by resolved preparations of *C. pasteurianum* hydrogenase, whereas addi-

tion of this metal does not affect methylene blue reduction.[4] Similarly, addition of MoO_3 to partially resolved preparations of *M. lactilyticus* hydrogenase affects the rate of benzyl viologen reduction markedly but has relatively little influence on methylene blue reduction.[16]

Since all systems which produce hydrogen from physiological intermediates also show evolution activity,[5] it would appear that a metal component permitting one-electron transfers is essential in normal H_2 formation by microörganisms. It is assumed that a low redox potential is required for this process (also for exchange activity), and it is possible that molybdenum may be of particular significance in this regard. Thus it has been suggested that the low E_0' value (-0.45 volt) of the iron-molybdoflavoprotein xanthine oxidase may reflect a contribution of molybdenum to the potential.[10] The remarkable similarity of hydrogenase to milk xanthine oxidase has previously been noted.[4, 10]

The state of iron in hydrogenase is assumed to be ferrous for three reasons: (*a*) CO combines only with the ferrous form of iron enzymes;[18] (*b*) cyanide, which specifically affects the ferric state, does not significantly inhibit hydrogenase activity under strictly anaerobic conditions (e.g., see Hyndman, Burris, and Wilson[8] and Hoberman and Rittenberg[12]); and (*c*) the enzyme is very susceptible to inactivation by oxygen and other oxidizing agents.[1, 21] Evidence recently furnished by Fisher *et al.*[13] indicates that the hydrogenase of *P. vulgaris* can be inactivated by *oxygenation* and that this type of inhibition is reversed by physical or chemical means. These considerations suggest that the initial activation of H_2 may occur by a reaction analogous to that described by Klotz and Klotz[22] for the oxygenation of the iron protein hemerythrin. Further studies with purified hydrogenases will be required for a more detailed understanding of the initial reaction and the subsequent electron-transport pathways.

SUMMARY

The isotope exchange reaction between heavy water and molecular hydrogen has been measured in a number of different microbial hydrogenase preparations and has been compared with their ability (*a*) to reduce methylene blue with H_2 and (*b*) to produce H_2 from reduced methyl viologen. Certain preparations showing hydrogenase activity only by methylene blue reduction fail to catalyze the exchange reaction at an appreciable rate. Special importance is attributed to the correlation between absence of exchange activity and inability to evolve hydrogen from reduced methyl viologen. Additional evidence implicating iron as an essential component of hydrogenase is cited, and a generalized formulation of the mechanism of action of the enzyme is presented.

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PIGMENT CONVERSION IN THE FORMATIVE RESPONSES OF PLANTS TO RADIATION

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Many aspects of growth and maturation of plants are known from the close similarity of their action spectra to be controlled by a reversible photoreaction.[1] Among these responses are germination of seeds of some higher plants[2] and of fern spores,[3] photoperiodic control of flowering,[4] coloration of some fruits,[5] and etiolation.[6] The photoreaction can be written as follows:

$$\text{Pigment}_1 + (\text{A reactant}) \underset{\text{Far-red radiation (Max. near 7350 A) or Darkness}}{\overset{\text{Red radiation (Max. near 6600 A)}}{\rightleftharpoons}} \text{Pigment}_2 + (\text{Changed reactant})$$

(red-absorbing) (far-red absorbing)

The essential contribution herein is the expression of the physiological response as a function of the fractional conversion of the pigment into the effective form,

whichever that may be, and the finding of minimum values for the products of the respective absorption coefficients and the quantum efficiencies for conversion of the two pigment forms in vivo. These ends are attained without knowledge of the chemical nature of the pigment or of its concentration. The method depends upon physiological information and upon the fact that the photoreaction is reversible and follows first-order kinetics with respect to energy in both directions. That the reaction rate is not limited by molecular collision in either direction is shown by temperature coefficients of unity for the photoreactions in both directions for germination of lettuce seed between 6° and 26° C.[7]

The method of analysis is similar to the one used by Warburg and Negelein[8] to find the products of the absorption coefficients and quantum efficiencies for dissociation of cytochrome oxidase–carbon monoxide by photoreversal in vivo of the poisoning with carbon monoxide of the respiration function of the oxidase.

After irradiation with energy E in an absorption region $\lambda_1 \pm \Delta\lambda_1$, an unknown fraction F of the pigment in one form is converted to the other according to the differential equation $dF/dE = k(1 - F)$. The solution of this equation is $kE = \log [1/(1 - F)]$. If the energies required to give two physiological responses, 1 and 2, have the relationship $\alpha = E_2/E_1$, then $\alpha \log [1/(1 - F_1)] = \log [1/(1 - F_2)]$. The same responses in the reverse direction, obtained with the energies of the reversing radiation in an absorption region $\lambda_2 \pm \Delta\lambda_2$, will have a different ratio β, with $\beta \log [1/F_2] = \log [1/F_1]$. Thus, if α and β are measured for any two arbitrary degrees of physiological expression, values of F_1 and F_2 can be calculated. The only limitation for the equations as set up is that the dark reaction be slow and the radiant energy used for one response be relatively free of that inducing the other, but $\Delta\lambda$ need not be small.

The products of the absorption coefficients, ω (cm²/gram molecular weight), and the quantum efficiencies, ϕ, for both the red and the far-red form of the pigment can be determined from the fraction, F, of the pigment converted in a given spectral region by a given incident energy E (in einsteins/cm²). Thus $\omega\phi X$ = number of effective quanta = F/E, where X is the fraction of the incident energy reaching the region of absorption. The molar extinction coefficient, in American usage, is $[\omega/1{,}000] \log_e 10$.

Internode elongation of the bush Pinto bean is the first example considered. If these beans are grown with daily light periods of several hours under light sources such as "white" fluorescent lamps having low intensities in regions beyond 7000 A, the developing internodes are short. But if they are exposed after the end of each light period on four successive days to moderate energies, which can be delivered in a few minutes or less, in the region beyond 7000 A the internodes increase in length several fold; essentially the beans are changed from "bush" to "pole" at this stage of growth. If the plants are irradiated with red light following exposure to high energy in the far-red region of the spectrum at the end of the light period, the lengthening stimulus of the far red is nullified. The internodes may attain lengths, depending on the red energies, no greater than those of control plants. This is the reversal. Essentially the length of the second internode of the bean is a function of the fraction of the pigment converted by radiation, and it can be used as an index of the conversion irrespective of the nature of the function.

Results of an experiment are given in Table 1. The mean internode lengths are the averages for lots of 24 plants. If two responses are taken as the internode

lengths 40.3 and 65.2 mm., respectively, the value of β for far-red radiation is 8.00/4.00 = 2.00. From interpolation on a plot of the third columns against the first columns, the reverse times to give the two internode lengths with the arbitrary red

TABLE 1

MEAN LENGTHS OF SECOND INTERNODES OF PINTO BEANS RESULTING FROM IRRADIATIONS FOR VARIOUS PERIODS WITH FAR-RED RADIATION AND WITH RED RADIATION FOLLOWING SATURATING FAR-RED EXPOSURES

PERIODS OF IRRADIATION (MIN.)*	MEAN INTERNODE LENGTHS FOLLOWING IRRADIATION (MM.) Far-red	Red	PERIODS OF IRRADIATION (MIN.)*	MEAN INTERNODE LENGTHS FOLLOWING IRRADIATION (MM.) Far-red	Red
0.00	26.3	88.0	2.00	31.7	59.6
0.25	27.0	86.6	4.00	40.3	50.3
0.50	28.7	81.3	8.00	65.2	35.0
1.00	29.6	77.5	16.00	96.0	30.7

* Each radiation source had a power equivalent to about 0.25 milliwatt/cm² at the wave length of maximum action integrated over the region of action.

radiation source are 5.95 and 1.63 minutes, respectively, giving $\alpha = 5.95/1.63 = 3.65$. The corresponding solutions of F_1 and F_2 are 0.10 and 0.316. A measure of precision is indicated by calculation for $\beta = 2.00$ and $\alpha = 3.30$ or 4.00. The respective values of F_1 and F_2 are 0.12 and 0.348 and 0.08 and 0.284. The value of k for the far-red irradiance is accordingly 0.35 per minute of irradiation. The complete curve of physiological response as a function of pigment conversion by far-red radiation as calculated for this value of k is shown in Figure 1. The fact that

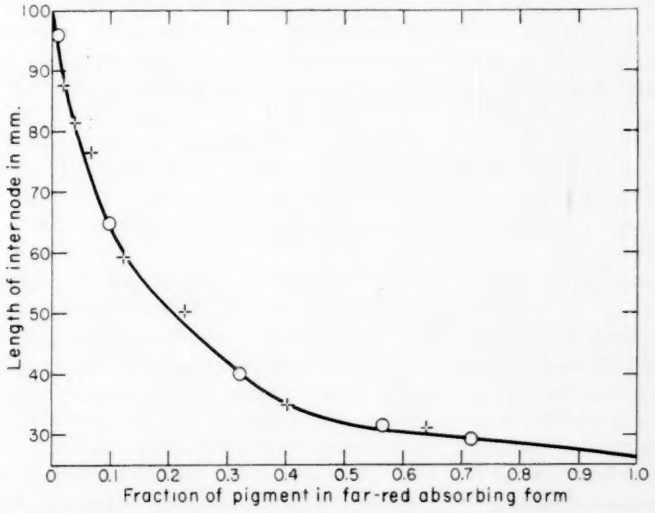

FIG. 1.—Internode lengths of Pinto beans as a function of pigment conversion: circles are for irradiation in the red part of the spectrum of beans with the pigment initially in the red-absorbing form, and crosses are for irradiation in the far red with the pigment initially in the far-red-absorbing form.

the points for both red and far-red radiation fall along the same curve validates the first-order kinetics.

Values of $\omega\phi X$ are next determined for the pigments in the spectral regions of

maximum action. These values are based upon internode lengths for beans from which one of the two primary leaves was removed so that the plants might be irradiated in a spectrum on four successive nights following their growth periods under fluorescent lights. One group of 18 plants was irradiated in the region 7100–7600 A and another group in the region 6300–6700 A after they had received a saturating exposure to far-red radiation. The first group received an incident energy of 9.1×10^{-7} einstein/cm^2 in each daily irradiation and the second 1.84×10^{-7} einstein/cm^2. The fractions of the pigment converted for the two groups were 0.81 and 0.21, respectively, as based on the variation of internode lengths of similar beans, with a single leaf, as a function of incident energy. The values of $\omega\phi X$ are 0.09×10^7 and 0.11×10^7 for the far-red and the red-absorbing forms of the pigment, respectively.

Before this procedure is extended to other examples, attention is again directed to the fact that the "mean" physiological response of bean internodes serves as an index of the pigment conversion. Each internode value listed in Table 1, for example, is a mean obtained from 24 individuals that varied in internode lengths. Reasons for the variations were many, including variation in the fraction of the pigment converted by a given incident energy.

The procedure used for analysis of internode growth may be applied with equal validity to germination of seeds, despite differences in the character of results obtained in the two cases. The length of an internode following a light treatment may have any value between that for the untreated and that for saturated control plants, but the response of a seed following light treatment is either germination or lack of germination. After red irradiation, some imbibed seeds germinate upon being held in darkness at a favorable temperature while others remain dormant. At a slightly higher red energy the germination requirements of these same seeds and those of an increment are met. The seeds of this increment are different from all others in that their energy requirements for germination are greater than the first energy given but less than the second. The crucial point is that the analysis is based only on such an increment, and this increment is the same whether reached by promotion of germination with red or inhibition of germination with far-red radiant energy.

The germination responses of lettuce, *Lactuca sativa*,[7] and of pepper grass, *Lepidium virginicum*,[9] seeds to an increasing series of red and far-red energies have been measured, as illustrated for *L. virginicum* in Figure 2. Action spectra giving the incident energies required for given percentage germinations are also known.[7, 9] All the information thus is available for calculations of the germination response as a function of the fractional conversion of the pigment and for finding the product of the absorption coefficient, the quantum efficiency, and X, that is, $\omega\phi X$. The germination functions for the two kinds of seed as calculated are shown in Figure 3.

Lepidium seed imbibed in 0.2 per cent KNO_3 solution requires about 4.5×10^5 ergs/cm^2 at the action maximum of 6400–6600 A for 50 per cent germination at a constant temperature of 20° C. This per cent germination requires 0.17 conversion of the pigment. An energy of 7.0×10^4 ergs/cm^2 at the action maximum of 7200–7500 A is required for 50 per cent inhibition of fully promoted seed. The values of $\omega\phi X$ calculated from these quantities are 0.067×10^7 for the red-absorbing form of the pigment and 1.9×10^7 for the far-red-absorbing form. For lettuce seeds

these values are 5.0×10^7 and 0.11×10^7, respectively, with 50 per cent germination corresponding to 50 per cent pigment conversion.

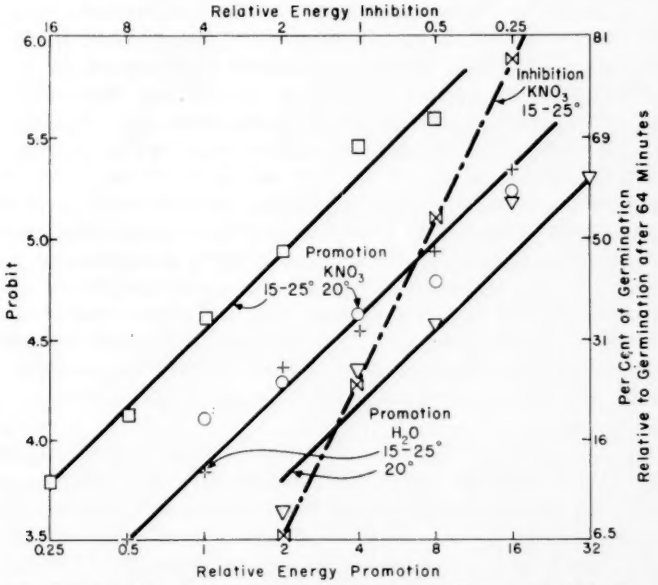

FIG. 2.—Variation in germination of *Lepidium virginicum* seeds with times of irradiation for promotion in the red part of the spectrum and with inhibition in the far-red after full promotion. Conditions under which the seeds were held are indicated.

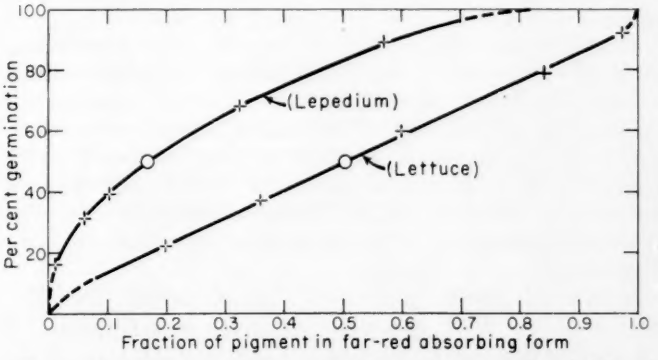

FIG. 3.—Variation in germination of *Lepidium virginicum* seeds and of Grand Rapids lettuce seeds with pigment conversion. The circles represent the interpolated values for 50 per cent germination.

An immediately evident fact is that the values of $\omega\phi X$ vary for the several objects, but the question whether the variation is in ω, ϕ, or X involves further considerations. These considerations can be based on results for germination of *L.*

virginicum seed as reproduced in Figure 2. As conditions affecting germination are varied, the several lines expressing promotion of germination as a function of incident energy are displaced without change of slope. This means that the fraction of pigment converted for a given germination is constant but that the incident energy required for this conversion varies. Since the seed is not changed in its light-absorbing or light-scattering characteristics by the several conditions, X is approximately constant. The conclusion is that ϕ, the quantum efficiency for pigment conversion, varies with conditions of seed germination. A deduction to account for variation in ϕ is that a reactant other than the pigment is involved in the photoreaction in both directions.

A probable maximum value of the quantum efficiency for pigment conversion per chromophoric group is 1.0. The value of X also cannot be greater than 1.0, and an order of magnitude for seeds and leaves would be in the range of 0.1–0.5 or less. The maximum values found for $\omega\phi X$ are 5.0×10^7 for red absorption in lettuce seed and 1.9×10^7 for far-red absorption in *Lepidium* seed. The minimum value of the molecular absorption coefficients of the pigment, $\omega/1{,}000$, in both forms at the action maxima, then, are of the order of 10^6. The oscillator strengths, accordingly, are of the order of 1.0, the intrinsic time constant of the excited states being of the order of 10^{-9} second.

The values of absorption coefficients of the two pigments in the region between 4000 and 5200 A are of the order of 0.01 times those at the action maxima in the red and far-red portions of the spectrum. This was shown[7] by the rate of approach with increasing radiant energy to an equilibrium physiological response in the region 4000–5200 A of objects in which the pigment systems were displaced to the two extremes by absorption in the red or far red. The method is independent of possible overlapping absorptions. The significance here is that cyclic tetrapyrolle systems, such as are present in porphyrins and might naturally be suspected here, are eliminated as possibilities for the pigment structures on account of their strong absorptions in the region in question. Instead, the pigments are probably open-chain conjugate systems, which include the phycocyanins of the blue-green algae as possibilities. The molecular extinction coefficient of c-phycocyanin at the absorption maximum of 6150 A is 2.76×10^5 as measured by Svedberg and Katsurai.[10] The corresponding probable value of the molecular absorption coefficient referred to a single chromophoric group is 1.59×10^5, based on four groups in each molecule. Allophycocyanin has an absorption maximum at 6500 A[11] and its relative absorption coefficients at other wave lengths correspond closely to those of the red-absorbing form of the pigment. Polyenes, of types as yet unknown, are not excluded as possible structures of the pigments.

The details of the photochemical reaction are of interest. With the reactant's presence now demonstrated, its general nature can be anticipated. The photochemical reaction probably involves the radiationless transition of the molecule from an excited singlet- to a triplet-state. The triplet-state free radical probably accepts hydrogen from the reactant in one form and donates hydrogen to the oxidized reactant in the other form. The variations in quantum efficiency arise from the variations in the ratio of the oxidized and reduced forms of the reactant in the biological object depending upon ambient conditions. For the photoreaction to be first order with respect to energy in the presence of the reactant implies con-

tinuous association of either the oxidized or the reduced reactant and the pigment, as is characteristic of condensed systems.

The pigment in its far-red-absorbing form is evidently biologically effective. This deduction rests on three arguments, none of which is rigorous. The first argument is that, in two of the three objects considered, half-maximum physiological response was obtained with conversion of the order of 0.1 of the pigment from the red- to the far-red-absorbing form, and conversion of 0.75 approached physiological saturation. This type of dependence upon the fraction of the active far-red-absorbing form corresponds to that usually found in enzymatic control of a reaction. The second argument rests upon the fact that some seeds with the pigment in the red-absorbing form will lie dormant for about a century but will germinate in a few days when exposed to light, with consequent appearance of the far-red-absorbing pigment form. Inhibitors of germination present in seeds usually disappear after a year or more, so that discharge of the final dormancy would seem to depend upon the far-red-absorbing pigment form acting as an activator rather than the red-absorbing form acting as a suppressor of an inhibitor. The third argument is that photoreversibility in photoperiodism is lost, an indication of biological change, shortly after the pigment is converted to the far-red-absorbing form.

The pigment is not sensitive to destruction by photo-oxidation in either of the two forms. It is freely available for photoconversion. This follows from the fact that the pigment system was fully effective in the green bean leaf after an 8-hour light period at high energy, as shown by the results given in Table 1. During the day the fraction of the pigment in the far-red-absorbing form in plants growing in the open is determined by the ratio of the effective red and far-red radiation in the radiation from the sun and by the ratio of the oxidized to the reduced form of the reactant in the leaf. With darkness the far-red form of the pigment changes slowly by a thermal reaction toward an equilibrium with the red-absorbing form.[7]

Summary.—Variations of physiological response with the fraction of pigment conversion as obtained from the reversibility and the first-order character of the conversion with respect to energy in the controlling reversible photoreaction were measured for internode lengthening and seed germination. Knowledge of this fraction permitted calculation of absorption coefficients and quantum efficiencies for pigment conversion. The method is a general one applicable to photoperiodism and other responses controlled by the reversible photoreaction.

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*PROGRESSIVE CONFIGURATIONAL CHANGES, DURING CELL DIVISION, OF CELLS WITHIN THE APICAL MERISTEM**

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During the past several decades the three-dimensional shapes of cells which are essentially undifferentiated morphologically have been studied by a number of investigators. Many different organisms have been used. Some research has also been done on configurational changes, during cell division, in epidermal layers. Thus far, however, no analysis has been made anywhere of the shape changes, step by step, which take place during the course of cell division. Furthermore, no study whatever, from this standpoint, has heretofore been carried out on cells deep within a tissue. In view of the increased emphasis, both morphological and physiological, placed upon terminal and lateral plant meristems, the internal cells, within the stem apex, were chosen for this study of the progressive shape changes of dividing cells.

Previously comparisons have been drawn between the shapes of interphase cells and those of cells in division in the epidermis of the apical meristem of *Anacharis densa* (Matzke[1]); Mozingo[2] has traced the configurational alterations, during division, of epidermal cells of living roots of *Phleum pratense*. Various aspects of cell division have also been considered in a series of publications by Lewis.[3]

It is now known as a result of the research of numerous workers that cells which are essentially undifferentiated morphologically, in tissues, have an average of approximately 14 faces and that no one type is achieved. Much of the literature dealing with this has already been summarized (Matzke[4]). Cells with 8 hexagonal and 6 quadrilateral faces, as in the tetrakaidecahedra of Kelvin,[5] occasionally occur, but they are infrequent. In analyzing the factors responsible for shape determination, experiments have been performed on compression of lead shot by Marvin[6] and on bubbles in foam by Matzke.[7] Comparisons have been made between the shapes of cells in tissues and grains in a metal alloy by Williams and Smith[8] and by Smith.[9] Detailed analyses of similarities and differences in the data presented below and the results of previous investigators will be published elsewhere.

Materials and Methods.—Vigorously growing vegetative stem apices of *A. densa* were fixed in Craf, sectioned lengthwise at 40 μ, and stained in Feulgen and in ruthenium red. Only the median section of a tip was used, and it was examined under oil immersion with a Leitz Ortholux microscope. The cells were selected from the region of the apex above the visible origin of lateral primordia, and they were at least 4 cells from the periphery in any direction. This region is shown by the brace in Figure 1.

The 400 interphase cells tabulated below were taken from 193 stem tips, and the 400 dividing cells came from 329 apices. Some of the sections were utilized for both the dividing and nondividing cells. Since the slides could not be tilted under the microscope, the configuration of the individual cells was determined by careful and prolonged focusing up and down. Only those cells that could be unmistakably worked out in three dimensions were utilized, and consequently each median section yielded only one or a few cells that were clear and could be recorded. A freehand sketch was made of each cell used, showing all the contacts. Some of the cells were also illustrated with camera lucida drawings, eight of which are shown in Figures 2–9. These drawings are slightly schematized, and minor curvatures of the walls are not reproduced.

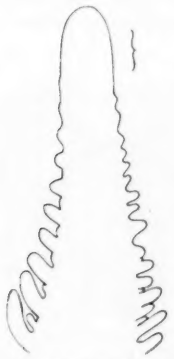


FIG. 1.—Camera lucida drawing of a longitudinal section of a stem tip of *A. densa*. The cells studied are in the region indicated by the brace. ×68.

The dividing cells were placed in seven groups according to the stage of division (Table 1). In early prophase (Fig. 3) the Feulgen stain was more intense than in interphase, and the chromatic material had become more evident. By middle prophase (Fig. 4) the chromosomes were more readily distinguishable, while in late prophase (prometaphase) the chromosomes were shorter and more deeply stained and the nucleoli and nuclear

TABLE 1

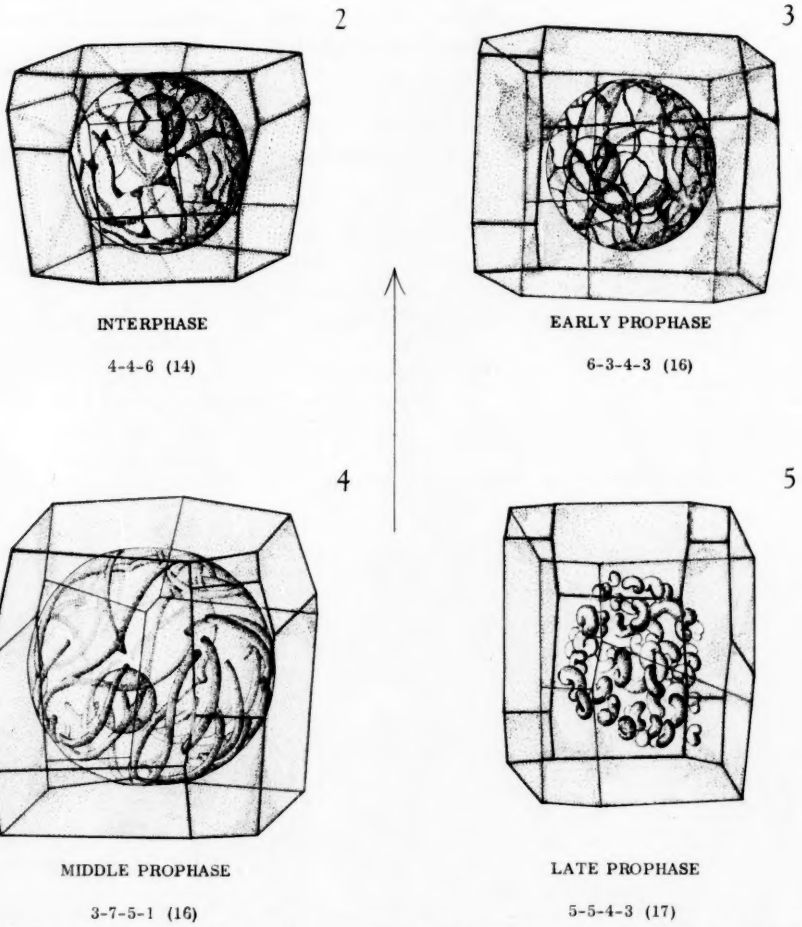
NUMBER OF FACES IN 400 INTERPHASE CELLS, IN 400 DIVIDING CELLS, IN VARIOUS STAGES OF DIVISION, AND IN 150 DAUGHTER CELLS, WITHIN THE APICAL MERISTEM (SHOOT APEX) OF *Anacharis densa* (ELODEA)

	No. Cells	No. Faces													Average
		9	10	11	12	13	14	15	16	17	18	19	20	21	22	
Interphase	400	1	7	22	61	78	101	70	28	21	6	4	0	1	..	13.85 ± 0.09*
Stage of mitosis:																
Prophase																
Early	60	..	..	..	..	1	2	13	17	13	10	3	1	0	0	16.43 ± 0.18
Middle	75	..	..	..	..	1	6	13	17	16	9	8	4	0	1	16.69 ± 0.21
Late	25	..	..	..	..	0	2	5	4	6	5	2	1	0	0	16.68 ± 0.32
Metaphase	60	..	..	..	..	1	2	9	19	11	10	1	4	3	0	16.82 ± 0.23
Anaphase	50	..	..	..	..	1	6	6	9	13	5	7	1	2	0	16.74 ± 0.27
Telophase																
Early	55	..	..	..	..	0	1	10	9	10	12	6	3	3	1	17.33 ± 0.25
Late	75	..	..	..	..	0	0	7	17	24	19	5	2	1	0	17.11 ± 0.14
Total dividing	400	..	..	..	..	4	19	63	92	93	70	32	16	9	2	16.84 ± 0.08
Daughter	150	..	3	20	54	40	24	6	3	..	..	..	..	.	.	12.61 ± 0.10

* Standard error of the mean.

membranes were no longer evident (Fig. 5). Metaphase and anaphase are illustrated in Figures 6 and 7 and were determined in accordance with the usually accepted criteria. Early telophase cells (Fig. 8) varied from those in which the cell plate was barely visible to those in which it nearly but not quite came in contact with the original walls of the parent cell. In late telophase (Fig. 9) it made contact with those walls.

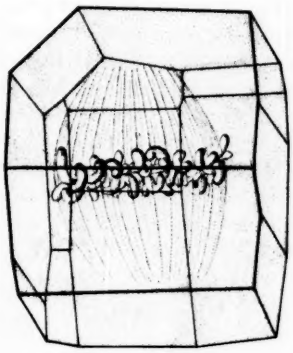
Data.—It is evident from Table 1 that the 400 interphase cells had an average of 13.85 faces and that the range extended from 9 to 21. Cells with 14, 13, 15, and 12 contacts occurred most commonly, in that order of frequency. An interphase cell with 14 faces is illustrated in Figure 2. The interphase cells recorded were not



FIGS. 2–5.—Camera lucida drawings, slightly schematized, of four characteristic cells, one in interphase and one each in early, middle, and late prophase. ×2,500. The formula for the combination of faces is given below each cell, i.e., 4-4-6 is 4 quadrilaterals, 4 pentagons, 6 hexagons, and the total number of faces for each cell is in parentheses. The cells, from different tips, are drawn in the same relative position, and the apex of the tips is indicated by the arrow.

in contact with dividing cells. The kinds of faces varied from triangular to nonagonal (Table 2), with hexagons, pentagons, and quadrilaterals by far the most abundant. The average number of faces for 1,150 cells in diverse tissues, previously studied by various investigators, was 13.86. These cells were presumably all in interphase.

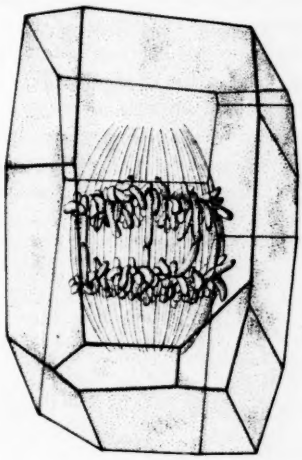
6



METAPHASE

4-6-6-0-1 (17)

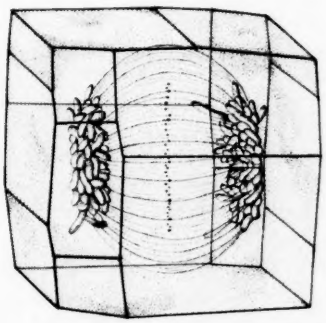
7



ANAPHASE

3-7-6-1 (17)

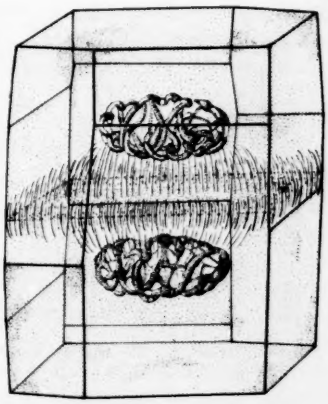
8



EARLY TELOPHASE

4-5-8-1 (18)

9



LATE TELOPHASE

5-2-5 (12)

4-5-7-1 (17)

5-3-4-1 (13)

FIGS. 6–9.—Camera lucida drawings, slightly schematized, of four characteristic cells, one each in metaphase, anaphase, early telophase, and late telophase. ×2,500. The formula for the combination of faces is given below each cell, and the total number of faces for each cell is in parentheses. In late telophase (Fig. 9) the formulas for the combinations of the two daughter cells into which the parent cell divided are also given. The cells, from different tips, are drawn in the same relative position, and the apex of the tips is indicated by the arrow.

The 400 cells referred to above occurred in 96 different combinations of faces, 12 of which are listed in Table 3. The most common combination, represented by 38 cells, had 4 quadrilateral, 4 pentagonal, and 6 hexagonal faces (4-4-6)—14 faces in all. One of these cells is illustrated in Figure 2. Other common combinations were 4-4-5, which was found in 28 cells; 4-4-4, which occurred in 25 cells; and 3-6-4, which was represented by 22 cells. These 4 combinations were also the most common in the 1,150 undifferentiated cells previously studied by various

TABLE 2

KINDS OF FACES IN 400 INTERPHASE CELLS, IN 400 DIVIDING CELLS, IN VARIOUS STAGES OF DIVISION, AND IN 150 DAUGHER CELLS, WITHIN THE APICAL MERISTEM OF *Anacharis densa*

	No. Cells	Tri-angular	Quadri-lateral	Pen-tagonal	Hex-agonal	Hep-tagonal	Octag-onal	Nonag-onal	Dec-agonal	Total
Interphase	400	5	1,605	1,837	1,844	239	10	1	0	5,541
Stage of mitosis:										
Prophase										
Early	60	1	249	322	326	73	15	0	0	986
Middle	75	8	306	418	394	101	22	3	0	1,252
Late	25	1	99	152	120	38	6	1	0	417
Metaphase	60	3	228	356	338	67	17	0	0	1,009
Anaphase	50	1	195	295	267	70	9	0	0	837
Telophase										
Early	55	0	233	300	327	80	13	0	0	953
Late	75	1	308	424	421	119	7	2	1	1,283
Total dividing	400	15	1,618	2,267	2,193	548	89	6	1	6,737
Daughter	150	4	597	691	506	91	3	0	0	1,892

TABLE 3

MOST FREQUENTLY OCCURRING COMBINATIONS OF FACES IN INTERPHASE, DIVIDING, AND DAUGHTER CELLS WITHIN THE APICAL MERISTEM OF *Anacharis densa*

Total Faces	Combination: No. Sides per Face 4	5	6	7	No. Cells* 400 Interphase	400 Dividing	150 Daughter
11	4	4	3	..	10^{10}	..	11^{3}
12	3	6	3	..	12^{8}	..	14^{2}
12	4	4	4	..	25^{3}	..	16^{1}
12	5	2	5	..	14^{5}	..	9^{4}
13	3	6	4	..	22^{4}	..	6^{5}
13	4	4	5	..	28^{2}	3	6^{6}
14	4	4	6	..	38^{1}	7^{8}	4^{14}
15	3	7	4	1	10^{11}	15^{1}	..
16	3	7	5	1	4	10^{4}	..
16	4	5	6	1	2	11^{2}	..
16	4	6	4	2	3	10^{5}	..
17	4	5	7	1	3	11^{3}	..

* Superior numbers indicate order of frequency.

authors. The 96 combinations of faces mentioned above were in 202 different arrangements, as determined by the construction of conventionalized models of each combination that was found more than once. In 27 arrangements there were 2 or more cells that were mirror images of each other Four of the 400 interphase cells had 6 quadrilateral and 8 hexagonal faces, as in the tetrakaidecahedra of Lord Kelvin. However, 20 other combinations occurred more often than the 6-0-8, and 4 others, in addition to the 6-0-8, were found four times, making 25 in all that were represented by 4 or more cells. It is evident, therefore, that there was no one predominant "type" in these interphase cells; that they varied in num-

ber, kinds, combinations, and arrangements of the faces, but within the general limits outlined above; and that only 1 per cent of the total had 6 quadrilateral and 8 hexagonal faces, as in the Kelvin tetrakaidecahedra.

The average of the 400 dividing cells was 16.84 faces (Table 1), the range extending from 13 to 22. Cells with 17, 16, 18, and 15 contacts occurred, respectively, most frequently. Pentagons, hexagons, and quadrilaterals were the most numerous, but other kinds of faces—heptagonal, octagonal, nonagonal, and triangular—were present far more often in the dividing than in the interphase cells (Table 2).

In Table 1 the number of faces is recorded for the stages of division. By early prophase the average had risen from the 13.85 of interphase to 16.43; in metaphase it was 16.82, and by telophase it was above 17. Thus the increase between interphase and early prophase was more than 2.5, while that between early prophase and telophase was definitely less than 1.

The 400 dividing cells occurred in 170 combinations of faces, of which 96 were found only once. The 5 found most frequently are listed in Table 3. The combination 3-7-4-1 was found fifteen times, 4-5-6-1 eleven times, and 4-5-7-1 eleven times, while 3-7-5-1 (Fig. 4) and 4-6-4-2 each occurred ten times. Unlike the commonest combinations of interphase and daughter cells, those in the dividing cells all had at least one heptagonal face. In these 170 combinations there were 366 different arrangements of the faces, of which 343 were each represented by a single cell. There was one cell, an anaphase, which had 6 quadrilateral and 8 hexagonal faces, as in the tetrakaidecahedra of Kelvin.

The 75 late telophase cells had cell plates which extended to the walls of the parent cells, so that the configurations of the 150 daughter cells thus formed could be determined. These 150 daughter cells had an average of 12.61 contacts, the range extending from 10 to 16 (Table 1). Twelve- and thirteen-faceted cells were most numerous. Pentagonal, quadrilateral, and hexagonal faces were more common than any other kinds (Table 2).

The 150 daughter cells showed 49 different combinations of faces, 24 of which were found just once, and 85 different arrangements of the faces. The combinations occurring most frequently (Table 3) were 4-4-4, 16 cells; 3-6-3, 14 cells; 4-4-3, 11 cells; 5-2-5, 9 cells; 3-6-4, 6 cells; and 4-4-5, 6 cells. All of these had only quadrilateral, pentagonal, and hexagonal faces. These were also common combinations in the interphase but not in the dividing cells.

The same daughter-cell combination was often derived from different parent-cell combinations. Thus 13 different parent-cell combinations, varying in number of faces from 15 to 18, gave rise to the 16 daughter cells with the combination 4-4-4, and 14 different parent-cell combinations gave rise to the 14 daughter cells with the combination 3-6-3. The 2 daughter cells derived from the same parent cell usually had different combinations of faces and nearly but not quite the same number of faces. Two such daughter cells, one with 12 and the other with 13 faces, are illustrated in Figure 9. One of the 150 daughter cells tabulated had 6 quadrilateral and 8 hexagonal faces, as in the Kelvin figures.

If the cell plate is hexagonal in outline, then the sum of the faces of the 2 daughter cells will exceed by 8 the number of faces of the parent cell, as in Figure 9; if the cell plate is pentagonal, the sum of the faces of the daughter cells will exceed those of the parent cell by 7; if heptagonal, the sum will be greater by 9, etc. Inspection

of Figure 9 shows further that in the division of a parent cell to form 2 daughter cells by means of a hexagonal cell plate, 6 faces are added to the contiguous cells, in addition to the 8 by which the sum of the faces of the 2 daughter cells exceeds the number of faces of the parent cell; in other words, division in this way results in the addition of 1 cell and a total of 14 faces to the cell mass. If the cell plate is pentagonal in outline, a total of 1 cell and 12 faces are added to the cell mass; if the cell plate is heptagonal, 16 faces are added to the cell mass. This occurs independently of the number of faces of the parent cell. In the 75 late telophase cells studied, 48 had hexagonal cell plates, 18 had heptagonal cell plates, and in 9 the cell plates were pentagonal. Therefore, a total of 14 faces was added to the cell mass of the growing apex as a result of the great majority of the cell divisions. This is in spite of the fact that 117 of the 150 daughter cells had fewer than 14 faces (Table 1), and it is independent of the total number of faces of the late telophase cells, which ranged from 15 through 21.

After interphase, dividing, and daughter cells (Table 1) had been recorded, a sampling was made to determine the ratio of dividing to interphase cells in the apical meristem. In the same limited region of the tip utilized for assembling the cells in Table 1, there were, in the median sections of 102 apices, 4,000 interphase cells and 322 cells in the various stages of division; 56 of these were in late telophase, and there were therefore 112 daughter cells. Utilizing the ratio of interphase, dividing, and daughter cells thus determined—including daughter rather than late telophase cells—and the averages established in Table 1, a weighted average was computed for all the internal cells of the stem tip. This weighted average was 14.0. While the exact number 14.0 may not be important, there can be little doubt that the internal cells of the stem apex of *Anacharis* have an average of 14, or of close to 14, faces when all are considered together.

Conclusions and Summary.—From the foregoing data it may be concluded that interphase cells within the apical meristem have an average of slightly less than 14 faces (13.85). No one type is achieved, since the 400 cells occurred in 96 different combinations of faces, some of which, however, were much commoner than others. There were 4 cells with 6 quadrilateral and 8 hexagonal faces, as in the tetrakaidecahedra of Kelvin, but 38, for example, with 4 quadrilaterals, 4 pentagons, and 6 hexagons (Table 3). Four hundred cells in various stages of division had an average of 16.84 faces. Most of the increase in number of faces occurs either prior to or by early prophase; a slight further increase takes place during the stages of division, and some additional contacts are also gained after the daughter cells have been formed. Swift[10] and several other investigators have reported that increase in DNA occurs in interphase preceding mitosis. The major increase in number of contacts in dividing cells is in essential agreement with this.

There is no one combination of faces which predominates during any of the stages of division, the 400 dividing cells having occurred in 170 combinations of faces.

The average number of faces for 150 daughter cells was 12.61—fairly close to that of the interphase cells. The combinations which occurred frequently in the daughter cells were also commonly found in the interphase cells but not in the cells in division.

Additional faces originate by division of contiguous cells; no evidence for "gliding growth" was obtained in the apical meristem.

It may further be concluded that cell division results in a plexus of diversified three-dimensional forms which arise from the interaction of numerous factors but that this occurs within fairly rigid mathematical limits. Inorganic systems which have previously been studied—bubbles in foams, compressed lead shot, grains in a metal alloy—show nothing which is comparable with the progressive configurational changes which characterize the stages of cell division. This would be expected, since cells originate in this intricate way from pre-existing cells. There is no one configurational "type" which is achieved, either in interphase, in division, or in the daughter cells resulting from division. When the numerous factors which play a part are considered—surface forces, contact and pressure, elasticity of the cell walls, directions of cell division, volume relationships of the cells, unequal growth of the cells, necessities of spherical geometry, and inherited form tendencies —no one "type" would be expected. In spite of this, there are both regularity and order, as indicated above, and the variation and spread which do occur are within definite limits, as the results show. These limits are in general more circumscribed than those in inorganic systems.

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*THE OPTICAL ROTATORY POWER OF HELICAL MOLECULES**

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Interest in the physical properties of helical molecules has increased in recent years, largely because of the helical configuration of many polypeptide chains. Since a helix has no elements of reflection symmetry, a molecule with a helical configuration is optically active even in the absence of asymmetric carbon atoms. In this article we shall apply the polarizability theory of optical activity to the determination of the specific rotation due to the helical configuration for an infinitely long helical molecule.

According to the polarizability theory of Kirkwood,[1] the specific rotation of plane-polarized light of sodium D wave length by an optically active compound is given by

$$[\alpha]_D = 4.930 \times 10^5 \frac{(n^2 + 2)g}{3M}. \quad (1)$$

Here n is the index of refraction of the solution, and M is the molecular weight of the compound. For molecules having substituent groups with polarizability tensors of cylindrical symmetry, the molecular rotatory parameter g is given by

$$g^{(0)} = \frac{1}{6} \sum_{i>k=1}^{N} \alpha_i \alpha_k \beta_i \beta_k G_{ik} \boldsymbol{R}_{ik} \cdot (\boldsymbol{e}_i \times \boldsymbol{e}_k),$$

$$G_{ik} = \frac{1}{R_{ik}^3} \left[\boldsymbol{e}_i \cdot \boldsymbol{e}_k - 3 \frac{(\boldsymbol{e}_i \cdot \boldsymbol{R}_{ik})(\boldsymbol{e}_k \cdot \boldsymbol{R}_{ik})}{R_{ik}^2} \right], \quad (2)$$

$$\boldsymbol{R}_{ik} = \boldsymbol{R}_k - \boldsymbol{R}_i.$$

The molecule is divided into groups each of which has a polarizability tensor of cylindrical symmetry, and the summation in equation (2) is taken over each pair of groups. $\boldsymbol{R}_i$ is the vector drawn from the center of mass of the molecule to the center of mass of the ith group, $\boldsymbol{e}$ is the unit vector along the axis of optical symmetry of the group, α is the mean polarizability of the group in cubic angstroms, and β is the anisotropy ratio of the group.

The centers of mass of the atoms forming the main structural chain are placed on a right-handed cylindrical helix whose equations are $x = a \cos \theta$, $y = a \sin \theta$, and $z = b\theta$. In equation (2) $\boldsymbol{R}$ is taken as the distance from the origin to a point on the helix. We shall consider here only cases where the polarizability tensors are symmetrical about the tangent to the helix. Therefore, the unit vector $\boldsymbol{e}$ becomes the unit tangent to the helix and is given by $d\boldsymbol{R}/ds$, where ds is an element of arc length. A case where the symmetry axis of the polarizability tensor is perpendicular to the helix has been discussed elsewhere.[2]

In applying equations (1) and (2) to helical molecules, we assume that the polarizability is continuously distributed over the length of the helix. The summation may then be replaced by an integration over the variable θ, so that

$$g^{(0)} = \frac{\alpha^2 \beta^2}{12} \int_0^{\theta_L} d\theta_k \int_0^{\theta_L} G_{ik} \boldsymbol{R}_{ik} \cdot (\boldsymbol{e}_i \times \boldsymbol{e}_k)\, d\theta_i, \quad (3)$$

where α is the mean polarizability per unit radian and β is the anisotropy ratio. Both α and β are assumed to be constant along the helix. The limits of integration are zero and θ_L, the total angle of revolution. The factor $1/2$ is introduced because the double integral counts each pair of angle elements twice.

The trigonometric functions in $g^{(0)}$ combine, so that the expression becomes a function of $\theta_{ik} \equiv \theta_k - \theta_i$ only. Letting γ equal b/a, we find that

$$g^{(0)} = \frac{\alpha^2 \beta^2 \gamma}{12a^2(1 + \gamma^2)^2} \int_0^{\theta_L} d\theta_k \int_0^{\theta_L} f(\theta_{ik})\, d\theta_i, \quad (4)$$

$$f(\theta) = \frac{\theta \sin \theta - 2(1 - \cos \theta)}{[2(1 - \cos \theta) + \gamma^2 \theta^2]^{5/2}} \left[\cos \theta + \gamma^2 - \frac{3(\sin \theta + \gamma^2 \theta)^2}{2(1 - \cos \theta) + \gamma^2 \theta^2} \right]. \quad (5)$$

The double integral in equation (4) is easily replaced by

$$\int_0^{\theta_L} d\theta_k \int_{\theta_k - \theta_L}^{\theta_k} f(\theta_{ik})\, d\theta_{ik},$$

which can be integrated by parts to yield

$$2\int_0^{\theta_L} (\theta_L - \theta_{ik})\, f(\theta_{ik})\, d\theta_{ik}$$

if $f(\theta_{ik})$ is even. In the following discussion, the subscripts on the variable θ_{ik} will be dropped for simplicity.

For an infinitely long helix, $\theta_L - \theta$ can be approximated by just θ_L, which equals $2\pi\nu$, where ν is the number of turns of the helix. The mean polarizability per radian, α, can be replaced by $\alpha_1/2\pi$, where α_1 is now the polarizability per turn. Unfortunately, $f(\theta)$ cannot be integrated analytically. However, for large θ, $f(\theta)$ may be approximated by

$$F(\theta) = \frac{[\theta \sin\theta - 2(1 - \cos\theta)](\cos\theta - 2\gamma^2)}{\gamma^3\theta^3},$$

which can be integrated analytically. The integral is therefore divided into two parts:

$$g^{(0)} = \frac{\alpha_1^2\beta^2\gamma\nu}{12\pi a^2(1 + \gamma^2)^2}\left[\int_0^{\epsilon} f(\theta)\, d\theta + \int_{\epsilon}^{\infty} F(\theta)\, d\theta\right]. \tag{6}$$

The first integral is evaluated by numerical integration. The second is integrated by parts until it reduces to the integral cosine,

$$Ci(\epsilon) = -\int_{\epsilon}^{\infty} \frac{\cos x}{x}\, dx,$$

the value of which can be obtained from tables.

Equation (6) is the most general expression for $g^{(0)}$ for an infinitely long molecule whose polarizability tensors are symmetric about a uniform cylindrical helix. We shall now apply equation (6) to a typical alpha helix with 3.69 amino acid residues per turn. The average radius a is 1.81 Å, and b is $5.44/2\pi$ Å.[3] If ϵ is taken as 6π, the first integral has a value of 0.467 and the second $Ci(12\pi) - Ci(6\pi)/\gamma^3$. If ϵ is greater than 6π, the result is substantially the same. Therefore, for a right-handed alpha helix,

$$g^{(0)} = 1.15 \times 10^{-3}\alpha_1^2\beta^2\nu,$$

$$[\alpha]_D = \frac{567\alpha_1^2\beta^2(n^2 + 2)}{3m}, \tag{7}$$

where m is M/ν, the molecular weight per turn.

To estimate the magnitude of the contribution to the optical activity by a helical structure, we shall compute the theoretical rotation of a hypothetical alpha helix of polyglycine, the only polypeptide having no asymmetric carbon atoms.

The mean polarizability for the various substituent groups of polyglycine is determined from the atomic refractions[4] by the relationship

$$\alpha_i = \frac{3}{4\pi N} \sum_s^{(i)} A_s. \tag{8}$$

The values of α_i in cubic angstroms are 1.81 for CH_2, 1.82 for C = O, and 1.42 for NH. If we assume that the mean polarizabilities are additive, the mean polarizability per turn, α_1, is 3.69 × 5.05 Å.[3] The anisotropy ratio β may be taken as about $^1/_3$ for the glycine residue, and the molecular weight per turn is 3.69 × 57.05. An estimated specific rotation for an infinitely long right-handed alpha helix of polyglycine in an aqueous solution with index of refraction 1.35 therefore is +132°.

The available experimental measurements of the optical activity of polypeptides cannot be applied to test the validity of equation (7) because these polypeptides are mixtures of right- and left-handed helices. Some polypeptides chains containing constituents with asymmetric centers may, because of asymmetric synthesis, attain a helical configuration in a preferential direction. However, the extent of this partial resolution, if it exists, is not known.

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HOMOLOGICAL DIMENSION IN NOETHERIAN RINGS

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1. *Introduction.*—It is our purpose in this note to present some new results in the theory of commutative Noetherian rings (with special emphasis on local rings) which we have obtained using the concepts and techniques of homological algebra, recently introduced by H. Cartan and S. Eilenberg. Since a more detailed account of these and other results will soon appear elsewhere, we take the liberty of omitting most proofs and bibliographical material.

2. *Preliminaries.*—Throughout this note, R will denote a commutative, Noetherian ring. If I is an ideal in R, we denote the rank of I by $\dim I$. We define $\dim R = \sup_I \dim I$, where I runs through all the ideals of R. By the integer $[I]$, we mean the smallest number of elements which generate I. We say that R is a local ring if R has a unique maximal ideal which we shall always denote by m. It is a classical result that $\dim R = \dim m \leq [m]$. R is called a regular local ring if $\dim R = [m]$.

Let M be an R-module. A projective resolution of M is a projective, acyclic complex X over M, i.e., a sequence of R-modules and R-homomorphisms,

$$\ldots \xrightarrow{d_{n+1}} X_n \xrightarrow{d_n} \ldots \to X_1 \xrightarrow{d_1} X_0 \to 0 \tag{2.1}$$

such that each X_n is a direct summand of a free R-module, $d_{n+1}(X_{n+1}) = d_n^{-1}(0)$ for all $n > 0$, and $X_0/d_1(X_1) \backsimeq M$. We define the homological dimension of M, h dim M, to be the smallest integer n such that there is a projective resolution of M with $X_{n+1} = 0$, if such an integer exists. Otherwise we define the homological dimension of M to be ∞.

A basic result concerning h dim M is that if $0 \to M' \to M \to M'' \to 0$ is an exact sequence of R-modules, with M projective and M'' not projective, then h dim $M'' =$ 1 + h dim M'.

The global dimension of the ring R, gl dim R, is defined to be the $\sup_M$ h dim M, where M runs through all R-modules. By a result of Auslander, we know that we may confine our attention to finitely generated R-modules.

3. *Codimension.*—Let R be a local ring with maximal ideal m. Cartan and Eilenberg have shown that if M is a finitely generated R-module, then h dim $M \leq$ h dim R/m. Therefore, we have the result that gl dim R = h dim R/m = 1 + h dim m.

3.1. LEMMA. *Let I be an ideal in the local ring R, and X an element in m such that $I:(x) = I$, where $I:(x) = \{r \in R / r\, x \in I\}$. Then h dim (I, x) = 1 + h dim I.*

Suppose now that R is a regular local ring of dimension n. Then R is an integral domain, and if $m = (u_1, \ldots, u_n)$, $(u_1, \ldots, u_i)$ is a prime ideal for each $i = 1, \ldots, n$. Therefore, from Lemma 3.1, we obtain

3.2. THEOREM. *If R is a regular local ring, then gl dim R = dim R.*

From Lemma 3.1 we can also deduce that m belongs to an ideal I in a regular local ring if and only if r dim I = h dim m.

Let I be a proper ideal in the ring R. We say that $x_1, \ldots, x_p \in R$ is an R/I-sequence if $I:(x_1) = I$, $(I, x_1, \ldots, x_i):(x_{i+1}) = (I, x_1, \ldots, x_i)$ for all $i = 1, \ldots, p-1$, and $(I, x_1, \ldots, x_p) \neq R$. If R is a local ring, it readily follows that the number of elements in an R/I-sequence is bounded and that $x_1, \ldots, x_p$ is a maximal R/I-sequence if and only if m belongs to $(I, x_1, \ldots, x_p)$. It is trivial to see that every R/I-sequence can be imbedded in a maximal one.

3.3. THEOREM. *If R is a local ring and I is an ideal in R, then all maximal R/I-sequences have the same number of elements.*

Proofs: Suppose that R is a regular local ring and dim $R = n$. Then $x_1, \ldots, x_p$ is a maximal R/I-sequence if and only if m belongs to $(I, x_1, \ldots, x_p)$, or, equivalently, h dim $(I, x_1, \ldots, x_p)$ = h dim m. But, by Lemma 3.1, h dim $(I, x_1, \ldots, x_p) = p$ + h dim I. Thus p = h dim m − h dim I, which proves the invariance of p. It is easy to see that the theorem is also true for all factor rings of regular local rings. If R is an arbitrary local ring, we know that $x_1, \ldots, x_p$ is a maximal R/I-sequence if and only if $x_1, \ldots, x_p$ is a maximal R^*/I^*-sequence, where R^* is the completion of R, and $I^* = R^*I$. Therefore, it suffices to prove the theorem for complete local rings. But every complete local ring is a factor ring of a regular local ring. *Q.E.D.*

An interesting consequence of Theorems 3.2 and 3.3 is that every regular local ring of dimension 2 is a unique factorization domain.

Theorem 3.3 leads us to introduce the following new invariants. We define the *codimension of R/I* (codim R/I), where I is an ideal in the local ring R, to be the number of elements in a maximal R/I-sequence. We can show that codim R =

$\sup_M$ h dim M, where M ranges over all finitely generated R-modules of finite homological dimension.

Note: Let R be a ring, and M an R-module. We define an M-sequence to be a sequence $x_1, \ldots, x_p$ of elements in R such that x_1 is not a zero division for M, and x_{i+1} is not a zero division for $M/(x_1, \ldots, x_i)M$, for all $i = 1, \ldots, p-1$. This is a direct generalization of an R/I-sequence.

4. *Regular Local Rings.*—Let R be a ring and S a multiplicatively closed subset of R not containing 0, and let R_S be the ring of quotients of R with respect to S. Since $\mathrm{Tor}_n^R(R_S, M) = 0$, for all $n > 0$, we have h dim$_R$ $M \geq$ h dim$_{R_S}$ $R_S \otimes_R M$. If I is an ideal in R_S, then $R_S/I \backsimeq R_S \otimes_R R/R \cap I$. Thus we have gl dim $R \geq$ gl dim R_S. Therefore, if R is a regular local ring and P is a prime ideal in R, then gl dim R_P is finite. It is well known that for regular geometric local rings, as well as for regular, nonramified complete local rings, R_P is also a regular local ring for every prime P. This observation, together with some direct computations, led the authors to conjecture

4.1. THEOREM. *A local ring R is regular if and only if gl dim R is finite.*

The proof of this theorem is a direct result of the following lemmas, the first of which was established by the authors and the second of which is an immediate consequence of a result of Serre.

4.2. LEMMA. *If R is a local ring of finite homological dimensions, then gl dim R = dim R.*

4.3. LEMMA. *If R is a local ring with maximal ideal m, then h dim $R/m \geq [m]$.*

4.4. COROLLARY. *If R is a regular local ring, then so is R_P for every prime ideal P in R.*

The last result leads one to say that a ring R is *regular* if and only if R_P is a regular local ring for all prime ideals P of R. For a regular ring R, we have gl dim R = dim R. If gl dim R is finite, it is clear that R is regular. Also, it is not difficult to show that all regular rings are finite direct sums of regular integral domains.

An ideal I in a regular ring R is said to be *perfect* if h dim R/I = dim I. Since h dim$_R$ $R/I \geq \sup_P$ dim P, where P ranges over all the prime ideals belonging to I, a perfect ideal is unmixed. We are able to establish the following version of the Cohen-MacAulay theorem:

4.5. THEOREM. *If R is a regular ring, and $I = (x_1, \ldots, x_n)$ is an ideal of rank n, then the $x_1, \ldots, x_n$ are an R-sequence regardless of the order in which they are written. Consequently, I is a perfect ideal and is therefore unmixed.*

It can also be shown that if dim $R \leq 2$, and R is a regular domain, then every minimal prime ideal in R is invertible.

We conclude this note with

4.6. THEOREM. *If R is a Zariski ring and M is an R-module, then h dim$_R$ $M \geq$ h dim$_{R^*}$ M^*, where R^* is the completion of R and M^* the completion of M. If R is a local ring, then the above inequality becomes an equality and gl. dim R = gl. dim R^*.*

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*GENERAL THEORY OF ELLIPTIC EQUATIONS**

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Let D be a distribution of compact carrier (support).[1] We shall study the question of when all distributions S which satisfy the equation

$$D * S = 0 \tag{1}$$

are real analytic functions (or indefinitely differentiable functions). In case D is a partial differential operator with constant coefficients, we shall give necessary and sufficient conditions on D in order that all the solutions of equation (1) be analytic (or indefinitely differentiable). Partial results in this direction were obtained by Petrowsky[2] and by Hörmander.[3] In the general case where D is a distribution of compact carrier, our results are not quite complete. However, we show that if all solutions of equation (1) are analytic, D is the composition of a translation with a partial differential operator, and then our conditions on D are necessary and sufficient.

Our method of proof of the sufficiency of the conditions is the construction of an elementary solution with the desired properties.[1] This elementary solution is constructed by means of the Fourier transform. The necessity of our conditions will be shown by exhibiting certain exponential sums which define distributions S satisfying equation (1).

We wish to remark that our method of deriving the sufficiency of our conditions by means of the elementary solution has a serious defect which explains why our results are not complete: there may exist distributions D of compact carrier for which all solutions of equation (1) are indefinitely differentiable but such that D has no elementary solution.[4]

Let R denote real Euclidean space of dimension n; C is complex Euclidean n-space. By C^1 we denote the space of all $z \in C$ such that $\Im(z_j) \geqq 0$ for all j. For l any rotation of C which maps R into R, we write C^l for lC^1. Let D be a distribution of compact carrier, and denote by P the Fourier transform of D, so that P is an entire function of exponential type on C which is slowly increasing on R. Let V denote the set of zeros of P in C; assume that $V \cap R$ is compact. We want to define an elementary solution for D in some sense as the inverse Fourier transform of $1/P$. There are two difficulties in doing this: the compact set of zeros $V \cap R$ and the convergence difficulty at infinity.

1. *The set* $V \cap R$.—It can be shown that, if K is any open neighborhood of V^* (a cube in R containing $V \cap R$) in C, then the map $PF \to \int_{V^*} F(z)\,dz$ is a continuous linear function on PA_K, where A_K is the space of functions analytic on K with the topology of uniform convergence on the compact sets of K, and $PA_K = \{PF\}_{F \in A_K}$ with the topology induced by A_K. Using the Hahn-Banach theorem, we can find a measure u on C of compact carrier such that, for $F \in A_K$, $\int PF\,du = \int_{V^*} F(z)\,dz$.[5] Suppose that $\int_{R-V^*} [1/P(z)] \exp(iz\cdot)\,dz$ converges in the space of distributions on R to a distribution T (say). Then it is readily verified that the sum of T and the inverse Fourier transform of u is an elementary solution for D.

Since u is a measure of compact carrier on C, the inverse Fourier transform of u is an entire function of exponential type and thus is as regular as we want.

2. *The set $R - V^*$.*—For each $x \in R$, denote by $\rho(x)$ the distance from x to V.

Condition a: $\lim_{|x|\to\infty} \dfrac{\log |x|}{\rho(x)} = 0.$

Condition b: There exists a $d > 0$ such that, for each $r > 0$ and for each l, we can find a real n-chain $\underline{\underline{\Gamma}}_r^l \subset C^l$ with the following properties:

(α) The boundary of $\underline{\underline{\Gamma}}_r^l$ is the boundary of V^*.

(β) The element of area on $\underline{\underline{\Gamma}}_r^l$ is $\leqq |x|^d\, dx_1 \ldots dx_n$ for $|x|$ large.

(γ) $|P^{-1}(z)| = 0(1 + |z|^r)$ in the chain in C lying between $\underline{\underline{\Gamma}}_r^l$ and R.

(δ) For $z \in \underline{\underline{\Gamma}}_r^l$, the distance from z to R is $\geqq r \log |z|$ for $|z|$ large.

It is easily seen that if P satisfies conditions a and b, then the integral $\int_{R-V^*} \exp(iz\cdot)[1/P(z)]\, dz$ converges in the space of distributions on R and is equal to $\int_{\underline{\underline{\Gamma}}_r^l} \exp(iz\cdot)[1/P(z)]\, dz$ for any l and r. Now suppose that $x \in R$, $x = (x_1, \ldots, x_n)$, $x_j > 0$, for all j. For $z \in \underline{\underline{\Gamma}}_r^l$, if $|z|$ is large, we must have, for some k, $\vartheta(z_k) \geqq \dfrac{r}{n} \log |z|$. Thus

$$|\exp(iz\cdot x)| \leqq \exp(-(z_k)x_k) \leqq \vartheta |z|^{-rx_k/n}. \tag{2}$$

From relation (2) we deduce easily that, for any $a > 0$, we can find an r so large that $\int_{\underline{\underline{\Gamma}}_r^l} \exp(iz\cdot)[1/P(z)]\, dz$ is a times differentiable in a neighborhood of x.

The case $x \in R$, $x \neq 0$, not all $x_j > 0$, may be easily reduced to the above by a linear transformation.

THEOREM 1. *Let D satisfy conditions a and b. Then all the distribution solutions of equation* (1) *are indefinitely differentiable functions. Conversely, if all the distribution solutions of equation* (1) *are indefinitely differentiable functions, then D satisfies condition a.*

Proof: If D satisfies conditions a and b, then the above implies that there exists an elementary solution for D which is an indefinitely differentiable function outside the origin. The fact that all solutions of equation (1) are indefinitely differentiable functions then follows without difficulty.[1]

Suppose that D does not satisfy condition a, and let[6] $F \in \mathfrak{D}$ be so chosen that $F(0) = 1$. We can construct a sequence of points $b^j \in V$ such that $|b^j + 1| - |b^j| \geqq 1$ for all j, and, for each l, $\sum_{j\neq l} j|F(b^l - b^j)| \leqq l/2$. Moreover, for some $a > 0$ and any k, $|\vartheta(b_k^j)| \leqq a \log |b^j|$, where we have written $b^j = (b_1^j, \ldots, b_n^j)$. We find easily that the series $\sum j \exp(ib^j\cdot)$ converges in the space $\mathfrak{D}'$ of distributions on R, say $U = \sum j \exp(ib^j\cdot)$. It is clear that $D * U = 0$. On the other hand, U cannot belong to the space $\mathcal{E}$ because, if f denotes the inverse Fourier transform of F, then the set $\{\exp(-ib^j\cdot)f\}$ is bounded in $\mathcal{E}'$, but

$$\begin{aligned} |U\cdot[\exp(-ib^j\cdot)f]| &= \left|\sum j\, F(b^l - b^j)\right| \\ &\geqq l|F(0)| - \sum_{j\neq l} j\,|F(b^l - b^j)| \\ &\geqq \frac{l}{2}. \end{aligned}$$

Thus $U \notin \mathcal{E}$, which completes the proof of Theorem 1.

If D has an elementary solution, we can show by use of the results of a previous paper[4] that condition b is a consequence of condition a. We have thus

THEOREM 2. *If D has an elementary solution, then all the solutions of equation* (1) *are indefinitely differentiable functions if and only if D satisfies condition a.*

We shall now study the analytic case.

Condition c: For some $\zeta > 0$, $\rho(x) \geqq \zeta |x|$ for $|x|$ large.

LEMMA. *If D satisfies condition c, then the carrier of D is one point, i.e., equation* (1) *is the composition of a translation with a partial differential equation.*

Proof: By multiplying P by functions of the form $P(z_1, \ldots, z_{j-1}, -z_j, z_{j+1}, \ldots, z_n)$, we obtain a function P^* which is invariant under $z_k \to -z_k$ for any k. By the theorem of addition of carriers, it is sufficient to show that P^* is a polynomial. For fixed $z_1, \ldots, z_{j-1}, z_{j+1}, \ldots, z_n$, we see that the function of one complex variable, $z_j \to P^*(z_1, \ldots, z_{j-1}, z_j, z_{j+1}, \ldots, z_n)$, satisfies condition c and thus must be a polynomial.[7] The result then follows.

By reasoning similar to that used in the proof of Theorems 1 and 2, we can deduce

THEOREM 3. *A necessary and sufficient condition that all distribution solutions of equation* (1) *be analytic functions is that D satisfy condition c. If this is the case, then equation* (1) *is the composition of a translation with a partial differential equation with constant coefficients.*

Example: For $k \geqq 2$, it is easily seen that the polynomial in two letters $z_1^{2k} + z_2^2$ satisfies condition a but not condition c.

The above can be extended without difficulty to systems of equations. Moreover, the classes "analytic functions" and "indefinitely differentiable functions" can be replaced by suitable classes of quasi-analytic and non quasi-analytic functions.

Added in proof: 1. In case D does not have an elementary solution, we can still show that, if D satisfies condition a, then there exists a linear function L on a suitable space of non-quasi-analytic functions, such that $D * L = \delta$, and such that L is an indefinitely differentiable function outside the origin. We can then deduce that condition a is necessary and sufficient in order that all distribution solutions of (1) be indefinitely differentiable functions.

2. In case D is a partial differential-difference operator which satisfies condition a, then we can show that the support of D is one point, so that equation (1) is equivalent to a partial differential equation with constant coefficients.

* Work supported by National Science Foundation Grant NSF 5-G1010 at the Institute for Advanced Study. The author is on leave from the Johns Hopkins University. The present note is a summary of results and methods; the details will appear elsewhere.

[1] L. Schwartz, *Théorie des distributions*, Vol. 1 (Paris, 1950).

[2] "Sur l'analyticité des solutions des systémes d'équations différentielles," *Mat. Sbornick*, **5**, 3–68, 1938.

[3] "On the Theory of General Partial Differential Equations," *Acta Math.*, **94**, 161–248, 1955.

[4] See L. Ehrenpreis, "Completely Inversible Operators," these PROCEEDINGS, **41**, 945–946, 1955, where a necessary and sufficient condition for the existence of an elementary solution is given.

[5] See L. Ehrenpreis, "Mean Periodic Functions. I," *Am. J. Math.*, **77**, 293–328, 1955, for the properties of the Fourier transform on the dual spaces of spaces of analytic functions.

[6] $\mathfrak{D}$ is the space of indefinitely differentiable functions of compact support on R; $\mathfrak{D}'$ is the space of distributions on R; $\mathbf{D}$ is the Fourier transform of $\mathfrak{D}$; $\mathcal{E}$ is the space of indefinitely differentiable functions on R; $\mathcal{E}'$ is the dual of $\mathcal{E}$.

[7] See L. Schwartz, "Théorie générale des fonctions moyenne-périodiques," *Ann. Math.*, **48**, 880. 1947.

*SPECTRAL SYNTHESIS FOR THE CANTOR SET**

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Let C denote the Banach space of bounded continuous functions on the real line with the norm, $\|\varphi\| = \sup_x |\varphi(x)|$. The spectrum[1] of a function $\varphi \in C$ is the closed set $\Lambda(\varphi)$ consisting of those points t such that $f \in L^1$ and $\int \varphi(x-y)\, f(y)\, dy \equiv 0$ imply $F(t) = 0$, where F is the Fourier transform of f, $F(s) = (2\pi)^{-1} \int \exp(-isx)\, f(x)\, dx$. Every closed subset of the real axis is the spectrum of some function in C.

The spectral synthesis problem is this: When is it true for a closed set T that $\varphi \in C$ with $\Lambda(\varphi) \subset T$ and $f \in L^1$ with $F(t) = 0$, for $t \in T$, imply $\int \varphi(x-y)\, f(y)\, dy \equiv 0$? Spectral synthesis on T is equivalent to the following statement: If I is a closed ideal in the L^1 convolution algebra over the reals and T is the set of zeros common to the Fourier transforms of functions in I, then every function in L^1 whose Fourier transform vanishes on T belongs to I. It is well known that spectral synthesis holds if the boundary of T contains no perfect set. Our aim is to show that the same is true when T is Cantor's ternary set. The proof is also applicable to other Cantor sets, including ones with positive measure.

Given $h > 0$, let $K_h(x) = 4h^{-2}x^{-2}\sin^2\frac{1}{2}hx$ when $x \neq 0$, $K_h(0) = 1$. For $\varphi \in C$, form

$$\Phi_h(t) = \int \exp(-itx)\, K_h(x)\, \varphi(x)\, dx.$$

$\Phi_h(t) = 0$ unless t is at a distance less than h from $\Lambda(\varphi)$.[2] Hence, if $\Lambda(\varphi)$ is compact, Φ_h vanishes outside a compact set, and the Poisson summation formula[3] may be applied to yield

$$\sum_{m=-\infty}^{\infty} K_h(x + 2\pi h^{-1}m)\, \varphi(x + 2\pi h^{-1}m) = (2\pi)^{-1}h \sum_{n=-\infty}^{\infty} \Phi_h(nh) \exp(inhx). \quad (1)$$

The sum on the left converges absolutely and uniformly in every compact set to a function $\varphi_h(x)$; the sum on the right is finite.[4] In particular, taking $\varphi \equiv 1$ in equation (1), $\sum K_h(x + 2\pi h^{-1}m) \equiv 1$. From this it is easy to see that, for any $\varphi \in C$, $\|\varphi_h\| \leq \|\varphi\|$ and $\varphi_h(x) \to \varphi(x)$ as $h \to 0$. Thus, for any $f \in L^1$,

$$\lim_{h \to 0} \int \varphi_h(x-y)\, f(y)\, dy = \int \varphi(x-y)\, f(y)\, dy. \quad (2)$$

If φ has a compact spectrum and F is the Fourier transform of f, it follows from equation (1) that

$$\int \varphi_h(x-y)\, f(y)\, dy = h \sum \Phi_h(nh)\, F(nh) \exp(inhx). \quad (3)$$

Now let T be Cantor's ternary set. We have to show that if $\Lambda(\varphi) \subset T$ and $F(t) = 0$ for $t \in T$, the right-hand side of equation (2) is zero. Let h tend to zero through the values 3^{-p} as $p \to \infty$. A number of the form $n \cdot 3^{-p}$ either belongs to T or is at a distance greater than or equal to 3^{-p} from it. Hence, whenever $h =$

3^{-p}, either $F(nh) = 0$ or $\Phi_h(nh) = 0$. Thus the sum on the right-hand side of equation (3) is identically zero. Combining equation (3) with equation (2), we have the desired result.

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[1] A discussion of the problem along with the necessary references will be found in Harry Pollard, "The Harmonic Analysis of Bounded Functions," *Duke Math. J.*, **20**, 499–512, 1953.

[2] See *ibid.*

[3] See S. Bochner, *Fouriersche Integrale* (Leipzig, 1932), p. 33.

[4] The Levitan polynomial. See N.I. Achieser, *Approximationstheorie* (Berlin, 1953), p. 146.

A CENTRAL LIMIT THEOREM AND A STRONG MIXING CONDITION

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Introduction.—This paper presents a central limit theorem for a sequence of dependent random variables

$$X_1, X_2, \ldots \quad .$$

The assumptions required are the usual assumptions on second and $2 + \delta$ order moments and a strong mixing condition. The theorem is of interest for two reasons. All general central limit theorems for dependent random variables formalize in some sense a heuristic notion of A. Markoff to the effect that one expects a central limit theorem to hold for $X_1, X_2, \ldots,$ if the random variables behave more like independent random variables the farther they are separated (assuming that appropriate moments exist). An interesting discussion of this intuitive notion is given in S. Bernstein's paper on the central limit theorem.[1] The strong mixing condition used in this paper seems to be a more intuitively appealing formalization of this notion than most others. The condition is also of interest because it is a strong version of the mixing condition encountered in ergodic theory (see Hopf,[2] p. 35).

The Mixing Condition.—The mixing condition is assumed to hold for sets of the form

$$a_{k_r} < X_{k_r} \leq b_{k_r}, \qquad r = 1, \ldots, s, \qquad (1)$$

where $k_1 < \ldots < k_s$. Given any two such sets A and B, introduce the following notion of distance $d(A, B)$ between them. Consider the smallest interval containing the indices of the random variables in terms of which A is defined. Call this interval $I(A)$. In the case of set (1), this interval is $[k_1, k_s]$. The distance $d(A, B)$ is set equal to the distance between the intervals $I(A)$ and $I(B)$. Note that $d(A, B)$ does not satisfy the usual properties of a distance; for example, one may have $d(A, B) > d(A, C) + d(B, C)$ for some set C. The strong mixing condition is satisfied by the sequence of random variables $X_1, X_2, \ldots,$ if

$$|P(A \cap B) - P(A)\,P(B)| < f(d(A, B)) \tag{2}$$

for all sets A, B of form (1), where $f(n)$ is a function defined for $n = 0, 1, 2, \ldots$, and decreasing to zero as $n \to \infty$.

The Central Limit Theorem.—Assume that the mean values $EX_k \equiv 0$, as one could in any case subtract the mean values EX_k from the random variables X_k, respectively. The assumptions are

1. $$E\left|\sum_{j=a}^{b} X_j\right|^2 \sim h(b-a)$$

as $b - a \to \infty$, where $h(m) \uparrow \infty$ as $m \to \infty$;

$$E\left|\sum_{j=a}^{b} X_j\right|^{2+\delta} = o(h(b-a)^{1+\delta/2}$$

as $b - a \to \infty$ for some $\delta > 0$.

2. The strong mixing condition (2) is satisfied by the sequence of random variables $X_1, X_2, \ldots$.

Introduce the following notation:

$$S_n = \sum_{j=1}^{n} X_j,$$

$$U_r = \sum_{j=(r-1)(p_n+q_n)+1}^{rp_n+(r-1)q_n} X_j,$$

$$V_r = \sum_{j=rp_n+(r-1)q_n+1}^{r(p_n+q_n)} X_j, \quad r = 1, \ldots, k,$$

where $k(p_n + q_n) = n$. The numbers k, p_n, q_n will be chosen in such a way that $p_n, q_n, k \to \infty$ and $q_n/p_n \to 0$ as $n \to \infty$.

We expect to show that

$$\frac{S_n}{\sqrt{kh(p_n)}}$$

is asymptotically normally distributed. Now

$$E^{1/2}\left|\sum_{r=1}^{k} \frac{V_r}{\sqrt{kh(p_n)}}\right|^2 \leq \sum_{r=1}^{k} \frac{E^{1/2}|V_r|^2}{\sqrt{kh(p_n)}}$$

$$\sim \frac{(kh(q_n)}{h(p_n))^{1/2}}.$$

Choose the sequences q_n, p_n, k such that

$$\frac{kh(q_n)}{h(p_n)} \to 0.$$

Then

$$\sum_{r=1}^{k} \frac{V_r}{\sqrt{kh(p_n)}} \to 0$$

in probability as $n \to \infty$. It can therefore be neglected in further computations. We shall later see that this can be done.

Set

$$G_{r,\,n}(x) = P\left\{\frac{U_r}{\sqrt{kh(p_n)}} \leq x\right\},$$

and let the set

$$\left\{m_r\delta < \frac{U_r}{\sqrt{kh(p_n)}} \leq (m_r + 1)\delta\right\} = A(r, n, m_r, \delta),$$

where m_r is an integer. Note that

$$\sum_{(m_1 + \ldots + m_k + k) \leq x} P\left(\bigcap_{r=1}^{k} A(r, n, m_r, \delta)\right) \leq P\left(\sum_{r=1}^{k} \frac{U_r}{\sqrt{kh(p_n)}} \leq x\right) \leq \sum_{(m_1 + \ldots + m_k)\delta \leq x} P\left(\bigcap_{r=1}^{k} A(r, n, m_r, \delta)\right) \tag{3}$$

LEMMA 1

$$P\left(\max_{r=1,\ldots,k}\left|\frac{U_r}{\sqrt{kh(p_n)}}\right| > t_k\right) < \epsilon$$

if $t_k = (k/\epsilon)^{1/2}$.

Now

$$E\left|\max_{r=1,\ldots,k}\left|\frac{U_r}{\sqrt{kh(p_n)}}\right|\right|^2 \leq E\left|\sum_{r=1}^{k}\left|\frac{U_r}{\sqrt{kh(p_n)}}\right|\right|^2 \leq k.$$

The result is obtained by an application of the Tchbycheff inequality.

LEMMA 2

$$\left|\sum_{(m_1 + \ldots + m_k)\delta \leq x} P\left(\bigcap_{r=1}^{k} A(r, n, m_r, \delta)\right) - \sum_{(m_1 + \ldots + m_k)\delta \leq x} \prod_{r=1} P(A(r, n, m_r, \delta))\right| \leq k\left(\frac{2t_k}{\delta}\right)^k f(q_n) + 2\epsilon.$$

The probability contributed by all the sets $\bigcap_{r=1}^{k} A(r, n, m_r, \delta)$ for which $\max |U_r/\sqrt{kh(p_n)}| > t_k$ is at most ϵ. Consider the sets $\bigcap_{r=1}^{k} A(r, n, m_r, \delta)$ for which $\max |U_r/\sqrt{kh(p_n)}| \leq t_k$. By repeated application of condition (2), one can see that

$$\left|P\left(\bigcap_{r=1}^{k} A(r, n, m_r, \delta)\right) - \prod_{r=1}^{k} P(A(r, n, m_r, \delta))\right| \leq kf(q_n).$$

Since there are $(2t_k/\delta)^k$ sets of this form, we obtain the desired inequality.

Let

$$G_{1,\,n} * \ldots * G_{k,\,n}(x)$$

be the convolution of $G_{1,n}(x), \ldots, G_{k,n}(x)$. Note that

$$G_{1,n} * \ldots * G_{k,n}(x) \leq \sum_{(m_1 + \ldots + m_k)\delta \leq x} \prod_{r=1}^{k} P(A(r, n, m_r, \delta)) \leq G_{1,n} * \ldots * G_{k,n}(x + k\delta) \tag{4}$$

and

$$G_{1,n} * \ldots * G_{k,n}(x - k\delta) < \sum_{(m_1 + \ldots + m_k + k)\delta \leq x} \prod_{r=1}^{k} P(A(r, n, m_r, \delta)) \leq G_{1,n} * \ldots * G_{k,n}(x). \tag{5}$$

Now $G_{1,n} * \ldots * G_{k,n}(x)$ tends to the normal distribution as $n \to \infty$ if $k \to \infty$. We want to let $k, p_n, q_n \to \infty$, $kp_n \sim n$, and $k\delta \to 0$ in such a way that

$$k\left(\frac{2t_k}{\delta}\right)^k f(q_n) \to 0 \tag{6}$$

$$\frac{kh(q_n)}{h(p_n)} \to 0. \tag{7}$$

Set $\delta = 1/k^2$. Then $k\delta \to 0$. Since

$$t_k = \left(\frac{k}{\epsilon}\right)^{1/2},$$

it follows that

$$k\left(\frac{2t_k}{\delta}\right)^k = k^{5/2k+1}\frac{2^k}{\epsilon^{1/2k}} \leq k^{5k}C^k,$$

where $C = 2/\epsilon^{1/2}$. The function f can always be chosen in such a way that $f(n) > 1/n$ for all n. If k is chosen so that

$$k \leq [-\log f(q_n)]^{1/2}, \tag{8}$$

clearly condition (6) will be satisfied.

Now

$$h(n) \sim E\left|\sum_{j=1}^{n} X_j\right|^2 \leq k^2 h\left(\frac{n}{k}\right)$$

by the Minkowski inequality. But then

$$\frac{k^2}{h(n)} \geq \frac{1}{h(p_n)}.$$

Thus

$$\frac{kh(q_n)}{h(p_n)} \leq \frac{k^3 h(q_n)}{h(n)}.$$

Condition (4) will then be satisfied if

$$h(q_n) = o\left(\frac{h(n)}{k^3}\right). \tag{9}$$

Sequences $k, p_n, q_n \to \infty$, $kp_n \sim n$ can be chosen so that conditions (8) and (9) are satisfied and hence conditions (6) and (7) are satisfied. On using inequalities (3), (4), and (5) and Lemma 2, we see that

$$\sum_{r=1}^{k} \frac{U_r}{\sqrt{kh(p_n)}}$$

is asymptotically normally distributed. Since

$$\sum_{r=1}^{k} \frac{V_r}{\sqrt{kh(p_n)}} \to 0$$

in probability as $n \to \infty$, it follows that

$$\frac{S_n}{\sqrt{kh(p_n)}}$$

is asymptotically normally distributed.

Remarks.—The result obtained includes the result of Höffding and Robbins.[3] It would be of very great interest to see how much stronger the notion of a strong mixing condition is than that of an ordinary mixing condition in the case of a strictly stationary process.

[1] S. Bernstein, "Sur l'extension du théorème limite du calcul des probabilités aux sommes de quantités dépendentes," *Math. Ann.*, **97**, 1–59, 1927.

[2] E. Hopf, *Ergodentheorie* ("Ergebnisse" series). J. Springer, Berlin, 1937.

[3] W. Höffding and H. Robbins, "The Central Limit Theorem for Dependent Random Variables," *Duke Math. J.*, **15**, 773–780, 1948.

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